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ARL ltr dtd 11 Dec 1969

ARL-TR-65-4

STUDY OF MONKEY, APE, AND HUMAN MORPHOLOGY AND PHYSIOLOGY RELATING TO STRENGTH AND ENDURANCE

PHASE V

THE MUSCULOSKELETAL ANATOMY OF THE ANTEBRACHIUM OF AN ADULT FEMALE CHIMPANZEE

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April 1965

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Certain of the animals used for this research were provided by the National Aeronautics and Space Administration under Order R-25.

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FOREWORD

This is the second in a series of four papers concerned with the musculoskeletal system of the thorax and upper extremities of the chimpanzee and the squirrel monkey. This study was conducted during the period 1961-1963 by William E. Edwards, under Contract AF 29(600)-3466, Project 6892, Task 689201. The program was monitored by Major James E. Cook, Veterinary Services Division, ARRV.

The author wishes to acknowledge the cooperation of Lt Col Hamilton H. Blackshear, Major Clyde H. Kratochvil, Major James E. Cook and Major Robert H. Edwards, all of the 6571st Aeromedical Research Laboratory. Mrs. Fogg-Amed assisted in the dissections and collaborated on the preparation of the drawings.

Publication of this report does not constitute Air Force approval of the report's findings or conclusions. It is published only for the exchange and stimulation of ideas.

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Major, USAF, MC
Commander

ABSTRACT

The left antebrachial musculature of a young-adult female chimpanzee is described and illustrated with the accuracy of detail plus clarity made possible by the photo-etching process. Other data are depicted graphically by section drawings. Comparisons with data from the literature on other chimpanzees, apes, humans, and non-hominoid primates are also provided, with emphasis on quantitative aspects.

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THE MUSCULOSKELETAL ANATOMY OF THE ANTEBRACHIUM OF AN ADULT FEMALE CHIMPANZEE

1. INTRODUCTION

The history of primate anatomy has been summarized in the writer's paper on the musculoskeletal anatomy of the thorax and brachium of the same chimpanzee specimen reported here (Edwards, 1965a).

In partial summary of the discussion in the aforementioned paper of the need for such anatomical studies, it may be observed that detailed, quantitative data on the chimpanzee are essential to such general interpretive problems as that of the phylogenetic history of man and his nearest relatives, as well as for such problems of application as those of analyzing the differences in chimpanzee and human function for experimental studies employing chimpanzees as analogs of humans. The writer's more specific interest in the anatomical research here reported is that of attempting to relate anatomical differences between chimpanzees and humans to the marked two-to-one superiority of the chimpanzee in strength of the upper extremities (Edwards, 1965b).

Although study of the thoracic and brachial musculature of the present subject was initiated seven weeks after its death in June, 1961, after amputation of its gangrenous right upper extremity, the left antebrachium was not studied until the spring of 1963, under an Aeromedical Research Laboratory contract.

Detailed data, including external measurements, on the young-adult chimpanzee subject, ARL Chimpanzee #133, are provided in the companion report (Edwards, 1965a).

2. PROCEDURE OF STUDY

The writer performed the dissections and took the photographs, with the assistance of Mr. Henry Phillips on several photographs. Mrs. Erika Fogg-Amed collaborated with the writer in producing the illustrations.

A detailed description of the general procedure of study is presented in the companion report, in which the photo-etching process, permitting extreme accuracy of detail, is described. The process of preparing drawings there reported was modified only to a limited extent. Since the

surface of one of the types of enlarging paper tested was found to be receptive to the uniform application of India ink without prior rubbing with powder, this step was temporarily discontinued. But much greater subsequent difficulty with "running" of ink lines during the bleaching process indicates the advantage of rubbing with talcum or, with more rapid effect, cleansing powder, while continuing to employ the ink-receptive double-weight enlarging paper ("Kodak Illustrators' Special E") as well. Pencil drawings over the photographs, as substitutes for somewhat more time-consuming drawings in India ink, were tested. Although the pencil lines survived the bleaching process satisfactorily, printing of such drawings photographically or with the "Xerox" duplicating process was found to be incompletely satisfactory. Alternatively, ink was applied over the pencil lines, but it tended to "bead," so this inking procedure also proved to be unsatisfactory.

The process eventually developed started with pencil drawings over the photographs. Unlike India ink, which necessitates damage to the photograph when erased (generally by scraping with a scalpel), pencil lines can be removed with perfect preservation of the underlying image (except for invisible furrows, which tend to deflect the pen upon subsequent application of fine ink lines). After series of corrections in pencil, the photographs were bleached. Following numerous additional corrections -- for it is impossible simultaneously to see the pencil lines and the photograph clearly in any but the lightest areas -- the pencil lines were erased one or two at a time and India ink lines were substituted. This process is very slow, but much more expeditious than the one used for the companion paper, for with the erasability of the pencil lines each illustration requires the preparation of only one or two drawings rather than the three or four typically required for the highest accuracy when using India ink alone. But despite the greater efficiency afforded during the preparation of this second paper, more than two thousand man-hours were expended on the combined chimpanzee anatomical research.

3. DESCRIPTION OF MUSCULATURE

A. Superficial Flexors

The superficial flexor musculature of the antebrachium is considered phylogenetically derived from the elbow matrix, and is thus related to brachialis and biceps, while the deep flexor muscles apparently migrated up from the area of the wrist, and are therefore related to the intrinsic hand muscles (Straus, 1942, p. 282).

The superficial (brachio-antebrachial) series, arising primarily from the medial epicondyle of the humerus, seems to manifest a moderately fundamental tripartite division into radial, intermediate, and ulnar sectors. Since this division "is recognizable in all tetrapods (and thus) must have

some real significance" (Straus, 1942, p. 282), the superficial flexors will be considered in that sequence.

Pronator teres. The uppermost muscle of the superficial group is the first of two muscles in the radial sector. The humeral head of pronator teres, constituting the heaviest forearm muscle in the immediate vicinity of the medial epicondyle of the humerus, arises from the proximal portion of the surface of the medial epicondyle and from a 13-mm.-long portion of the distal anterior border of the tendon of insertion of dorsoepitrochlearis (Figs. 1-3 and 5-11). The antero-ulnar surface of this muscle is entirely covered with a thick layer of tendon, an intermuscular septum which forms, with that of flexor digitorum sublimis, a v-shaped trough in which flexor carpi radialis and palmaris longis arise and traverse the proximal portion of the forearm (Fig. 16, U-V). The deeper supero-radial aspect is also covered 90 per cent near its proximal and 50 per cent near its distal ends with equivalently thick tendon; this tendon does not, however, constitute a septum for separation from contiguous muscles, for contiguous muscles are not significantly attached to it (Fig. 16).

An ulnar (deep) head of pronator teres also occurs, as in man. Arising from the coronoid process, it rapidly expands transversely but remains very thin, separated from the deep head of flexor digitorum sublimis by another intermuscular septum, a thick covering of tendon over its entire superficial surface. The median nerve traverses the hiatus between the two heads of this muscle. Shortly distal to its origin, the ulnar head, including its tendon, fuses with the humeral head; the tendon incompletely covers the proximal deep surface of the humeral head and continues distally between the two heads, separating them as a septum over much of the area of fusion (Fig. 16). More quantitatively, the two heads join 67 mm. from the proximal tip of the humeral head (and 20 mm. distal to the transection of that head depicted in Figures 9 and 10). Distal to the proximal tip of fusion, the much smaller ulnar head becomes thicker but narrower.

The joined heads insert upon the volar-radial aspect of the radius, beginning 110 mm. from the proximal end of the epicondylar (humeral head) origin and extending 95 mm. distally. The area of insertion on the radius is 94 to 189 mm. proximal to the distal tip of the radial styloid process and gradually narrows from a maximum width of 12 mm. near its proximal end. The ulnar head's superficial tendon is the first of the joined muscles to insert, 63 mm. beyond the aforementioned transection. At 30 mm. distal to the start of its insertion, the ulnar head becomes very thin; it feathers out altogether 85 mm. beyond the proximal tip of the insertion, just 10 mm. proximal to the distal tip of the humeral insertion.

Champneys (1871, p. 185) observed that the insertion of pronator teres in his chimpanzee was more distal than in man and that its origin was in part from dorsoepitrochlearis, like the current specimen, but

unlike that of Sonntag in this latter feature (1923, p. 348). Beddard (1891, p. 189) describes a "distinctly double" origin for pronator teres in his specimen, with a tendinous insertion on the radius some 63 mm. long. Keith (1899, p. 306) reports that the coronoid head is present in 9 of 11 chimpanzees but -- contrary to Pira's contention that almost all gorillas manifest it (1913, p. 329) -- in only 3 of 8 gorillas; for example, it was absent in Chapman's gorilla (1879, p. 55) and in von Bischoff's (1880, p. 12), but present in Raven's (1950, p. 43). This deeper head does not occur in most primates, such as the Hapalidae (Hill, 1957, p. 150); in fact, Parsons (1898, p. 735) asserts that it is limited to apes and man, although Straus reports apparently anomalous exceptions in a wide variety of mammalian species (1942, p. 285).

Flexor carpi radialis. Proximally, this muscle arises from the common flexor tendon in small part, but primarily from the septa lining the V-shaped trough between flexor digitorum sublimis and the humeral head of pronator teres -- a trough shared with palmaris longus superficially and ulnarly (Fig. 16, U-V). The fascicles on the ulnar side of this primarily bipennate muscle arise upon the septum -- fairly thick along the proximal half of flexor carpi radialis but grading to much thinner beyond the mid-point -- separating the muscle from flexor digitorum sublimis and, more superficially, from slender palmaris longus (Figs. 1-6, 8 and 11). On the radial side of the muscle, most of the area of contact with pronator teres is occupied by an intermuscular septum similar to that on the ulnar side. This septum extends distally toward the radius in an oblique fashion and terminates along the deeper portion of the contact area some 130 mm. from the proximal tip of flexor carpi radialis. Above its distal end, the septum fuses into a rather distinct narrow, thicker, more fibrous, tougher tendon-septum, which is very strongly adherent to the radius. Only some 5 mm. wide at the distal end of the broad septum (at 130 mm.), the tendon-septum gradually narrows to 3.5 mm. at the distal tip of pronator teres approximately 45 mm. beyond. The tendon-septum maintains fairly constant width and thickness as it extends down most of the remaining distal portion of the radius, terminating roughly 90 mm. beyond the distal tip of pronator teres. The fascicles on the radial half of bipennate flexor carpi radialis arise almost exclusively throughout its length from the narrow tendon-septum, which also provides insertion upon the radius for pronator teres.

The central tendon of insertion of the bipennate muscle becomes superficially apparent slightly above the level of distal termination of pronator teres. In accord with increasing tensile strength demands, it gradually thickens distally while it extends almost parallel to the main axis of the antebrachium -- although the concentration of the ulnar half of the muscle belly proximally and the radial half distally results in seemingly more marked obliquity toward the ulnar side as the muscle proceeds distally, with extension of the radial fleshy portion to the wrist area, some 60 mm. beyond the ulnar portion (Figs. 2 and 3). Essentially as in man, the tendon passes through the radial attachment of the transverse carpal ligament in a

synovial sheath and, according to Sonntag (1923, p. 348), inserts upon the palmar aspect of the bases of the second and third metacarpal bones.

Beddard (1891, p. 189) provides a description of a chimpanzee flexor carpi radialis in accord with observations on the present specimen. Sonntag (1923, p. 348) notes its "extremely long origin." In the present specimen, the most striking contrast of this specimen with the human condition is that, far from being restricted to the proximal two-thirds of the antebrachium, the muscle belly extends virtually to the distal tip of the radial styloid process.

Palmaris longus. On the radial side of the intermediate sector, this very slender muscle, whose fleshy portion and tendon in the area shown in the drawings (Figs. 1-6 and 8) weighs only 3.0 gm., occupies, in its proximal half, the right-angled, V-shaped trough between the superficial portions of flexor carpi radialis radially and flexor digitorum sublimis ulnarly (Fig. 16, U-V). The palmaris longus origin, fleshy throughout, is only in small part from its proximal termination at the medial epicondyle of the humerus; it attaches strongly to the dense superficial fascia of the antebrachium and to the proximal 115 mm. (40 per cent of the forearm length) of the fairly thin tendinous septa on both sides of the entire trough. These septa border virtually all of the muscle's fleshy portion. The septum on the ulnar side is continuous with the ulnar side of the deeper trough-septum of flexor carpi radialis (Fig. 6). The separate more radial septum, which apparently does not extend to and fuse to the superficial fascia along its entire length, is thinner and provides approximately two-thirds as much muscle-bundle origin as the more ulnar septum. The tensile strength requirements of the intermuscular septa, functioning as tendons of origin, are cumulative proximally -- much as the strength requirements of the tendon of insertion of this or other pennate muscles, such as flexor carpi radialis (see above), are cumulative distally. Accordingly, the proximal septa portions giving rise to muscle fascicles on both sides of palmaris longus manifest gradual thinning distally. Such distal thinning of the fascicle-attaching portions is also observable in other intermuscular septa of the antebrachium. Distal to the area of fleshy origin, the septa enclosing palmaris longus become markedly thinner and, comparable to other septa, decrease to extreme thinness where simply underlying the tendon of insertion.

The fleshy portion of the muscle, only 3 mm. wide at 5 mm. beyond the proximal end, gradually broadens to 6.5 mm. and thickens to 5 mm. as the trough widens and deepens.

A centrally located tendon of insertion of this bipennate muscle becomes visible at 108 mm. distally and gradually widens to 1.5 mm. as it shifts to the muscle's radial border at 130 mm. It continues to widen to 3.0 mm. as it extends down the radial border to the end of the fleshy portion, at 171 mm., and traverses without a fleshy concomitant the remaining 103 mm. shown in the drawings. Just before entering the wrist, it expands laterally to 5.2 mm.

and to a thickness of 1.6 mm. There, as shown in Figures 2-4, it fuses to the volar carpal ligament, which, in addition to the palmar aponeurosis, was apparently therefore regarded by Champneys (1871, p. 185) as an accessory area of insertion.

In Beddard's chimpanzee, palmaris longus was very similar in form, but apparently less distinctly separated proximally (1893, p. 189). In at least some chimpanzees it has been reported to be "well developed" (Chapman, 1879, p. 55). It was absent in both arms of Sonntag's specimen (1923, p. 348), as it was in three of the 12 chimpanzees considered by Keith (1899, p. 306). This apparently incipiently vestigial muscle manifests wide variability in many species, including the gorilla (Bischoff, 1880, p. 12) and man (Wood, 1867, pp. 56-57), in which it is absent in some 12 per cent of cases (Grant, 1947, p. 51; Hollinshead, 1951, p. 127). The muscle is distinctive of but not quite unique to mammals (Straus, 1942, pp. 291-292), and it is "almost as inconstant in the lower mammals as it is in man" (Parsons, 1898, p. 729).

Flexor digitorum sublimis. In the chimpanzee studied here, this muscle arises as four heads (Figs. 1-10 and 16). The proximal end of the origin of the radial head, which constitutes the most superficial head, is solely from the common flexor tendon at the medial epicondyle. As it proceeds superficially and fairly massively toward the mid-line of the wrist, the majority of its origin occurs from the thick antebrachial fascia and, as with the other superficial flexors, from the thick (relative to man's) tendinous septum extending continuously across its radial and deep surfaces; no such septum occurs on its ulnar aspect. At a point some 65 per cent of the distance from the proximal end to the wrist, the septum thins quite abruptly to approximately one-third of its more proximal thickness and strength, and it rapidly ceases its function of providing origin.

Beginning on its deep surface near the mid-line of this head in its proximal fifth, the major tendon of insertion gradually expands distally, achieving approximately its maximum breadth at 70 per cent of the distance to the wrist, but continuing to thicken as it shifts ulnarly, appearing to anterior view on the ulnar border some 220 mm. below the proximal tip of the muscle, which is 53 mm. above the distalmost point of the tendon shown in Figure 3; at this most distal point the tendon is 7.5 x 2.3 mm. On the radial side, fleshy muscle extends distally 6 mm. beyond this distalmost point shown in Figure 3.

The median head is unified with the radial head to approximately the middle of the forearm, but it is clearly observable as an entirely separate tendon, only loosely bound by very thin fascia, on the ulnar side of the larger head distal to a point some 185 mm. below the epicondylar tip of the radial head and 89 mm. above the distalmost point of both tendons exposed in Figure 3. This tendon extends above that point of separation, but the muscle bundles above the juncture-point run parallel to those below -- obliquely into the tendon -- and are all equally bound together superficially, without a natural plane of cleavage. On the deep

surface, however, the fascicles entering either side just above the junction-point are very readily separable to a depth of some two-thirds of the muscle thickness, and even beyond that they show easier cleavage until the superficial surface is closely approached. Thus in showing the deep surface of the two combined heads in Figure 8, the muscle is spread apart along this plane of cleavage (which the tendon parallels), some 85 per cent of the way through the muscle's thickness, for a better view of the tendons and fiber alignments, except where it is more tightly adherent in the first 25 mm. of the muscle below its proximal transection. The median tendon of insertion where cut near the wrist (Fig. 9) is 3.8 mm. wide and 3.2 mm. thick.

The ulnar head is a very thin muscle, shaped like a low isosceles triangle, with its long base extending longitudinally from its proximal tip two-fifths of the distance down the antebrachium. Only very thin fascia -- no more than one-twentieth as strong as the septa between the proximal portions of most of the flexor muscles -- binds it to the surface of flexor digitorum profundus along most of its ulnar border (Fig. 6). But in its proximal 35 mm., it is very adherent to the septum above it; this septum separates it from flexor carpi ulnaris and apparently provides the majority of its origin. At 10 mm. below its proximal end, it is 7.0 mm. wide and 1.6 mm. thick. At the point of maximum breadth, it is 21 mm. wide and 2.1 mm. thick. Its tendon of insertion is only 1.8 mm. x 1.5 mm. at the point where the ulnar head is transected (Fig. 9).

Figures 3 and 4 show the small portion of the ulnar head viewable upon removal of the superficial fascia. Figure 6 shows the muscle in its natural position, but with its proximal end obscured by fascia. In Figure 7, its radial half is pulled and folded back almost 180 degrees, while its tendon of insertion is twisted in Figure 8 to show the muscle's deep surface.

The deep head of flexor digitorum sublimis, which exhibits a very unusual essentially biventral form, arises ulnar to and moderately overlapped by the radial head and slightly by the most proximal portion of the radial border of flexor digitorum profundus, and its origin is deep to the thin, largely tendinous most proximal portion of flexor carpi ulnaris. It takes origin largely from the fairly thick ligament extending from the medial epicondyle to the olecranon process. For the first 40 mm. distal to the ligament of origin, it also arises from the ulnar portion of the intermuscular septum underlying the radial head of flexor digitorum sublimis, from the distalmost superficial tendon of brachialis, more from the broad superficial tendon covering the ulnar head of pronator teres (which underlies much of the proximal end of the deep head), and from the coronoid process. In its proximal 50 mm. of length, its dimensions throughout are almost identical to the only approximately 10 per cent more massive radial head. Where transected in Figure 9, some 45 mm. from its proximal end, it is 18.8 mm. wide by 12.3 mm. thick, entirely fleshy except for a thin strand of tendon on its radial-deep surface. The proximal tip of the thick tendon of origin of the distal belly appears slightly ulnar to its mid-line on the muscle's superficial surface 26 mm.

distal to the transection. The same tendon extends from the superficial surface through the proximal belly between its mid-line and its ulnar border and reappears on the deep surface as a narrow band, which appears 3 mm. more proximally than the superficial tendon sheet continuous with it on the opposite surface (Figs. 8 and 9). The proximal fleshy portion terminates at 46 and 49 mm. distal to the transection on the sides superficially and at 63 mm. on the mid-line deeply, where the tendon is 9.0 x 1.1 mm. The proximal tip of the distal fleshy portion occurs on the superficial surface at almost precisely the same point the proximal belly terminates deeply; the distal belly expands to either side and appears on the deep surface as narrow strips on either side of the broad tendon (of distal belly origin) 78 mm. distal to the proximal transection. On the deep surface, this broad tendon of origin extends to and even slightly beyond the distal transection depicted in Figure 9; throughout this length, it is flanked by narrow strips of distal belly on either side. This tendon broadens to 16 mm. at its widest point at almost precisely the mid-point of the distal belly. Because of its expanding width and reduced tensile strength requirements, this tendon of origin (although it simultaneously constitutes a tendon of insertion for the proximal belly) becomes progressively thinner distal to the proximal tip of the distal fleshy portion, until it is little more than a transparent membrane at the distal transection. The distal belly's tendon of insertion begins near the mid-line of the superficial surface 85 mm. distal to the proximal transection and continues with broadening to 11 mm. and then narrowing to 8.5 (x 2.9) mm. at the distal transection. The muscle's largest dimensions in the distal half are at 60 mm. above the distal transection, where it is 18 x 6 mm. At the end of the dissected area, its tendon of insertion goes into the wrist deep to and precisely at the center of the other three tendons of flexor digitorum sublimis.

The major portion (between the transections) of this unusual muscle weighed 11.2 gm. in 1963, when slightly dehydrated.

"The flexor sublimis digitorum appears to [vary in chimpanzees] considerably" (Sonntag, 1923, p. 348). Sonntag's specimen was apparently quite different from the one here reported, for it manifested "a very extensive origin from the humerus, ulna, and radius"; the "middle finger receives its tendon from a muscle arising from the lower two-thirds of the shaft of the radius" (Sonntag, 1924, p. 186). Champneys (1871, p. 185) also referred to a radial origin, not present in the specimen here studied, as did Beddard (1891, p. 189). "Flexor sublimis digitorum and profundus were more split up [in Chapman's chimpanzee] than in Man" (1879, p. 55). Beddard (1891, p. 189) described four heads; like the present specimen, "that supplying the little finger is very much more slender than the rest," the "stoutest tendon [commences] upon the under surface," and the tendon to the index finger is deep to the others. Since Sonntag's "coronoid head" was fusiform and also went to the second digit, it is quite surely comparable to the deep head in the specimen here studied, as is likely the "clearly defined 'two-bellied' muscle" of Fick's chimpanzee, which oddly constituted the deepest of three layers

of flexor digitorum sublimis (1925, pp. 122-123).

Flexor carpi ulnaris. This broad but relatively thin, bipennate muscle arises on the ulnar side of the origin of flexor digitorum sublimis from the posteromedial portion of the medial epicondyle (and thus of the common tendon) and the anteromedial portion of the olecranon; the intervening "saddle" is crossed by a fairly thick sheet of tendon underlain by a thin layer of fleshy muscle (Figures 2-6 and 16). A fairly thick, tendinous intermuscular septum underlies the muscle, separating it from the deeper radial and deep heads of flexor digitorum sublimis and, ulnarly, from flexor digitorum profundus; much of this septum is depicted in Figure 6. Near the epicondylar origin, this septum is especially thick and tendinous, and it separates from flexor carpi ulnaris and extends deep to the ulnar nerve in the area immediately below the epicondyle (Figs. 6-8). In its proximal seven-tenths, flexor carpi ulnaris is firmly attached to this septum, which thus apparently provides the majority of its origin. As is the case for all of the superficial flexors, there is also tight adherence to the fascia covering the arm. But there is no origin "from a considerable portion of the ulna," as reported by Beddard (1893, p. 189). Some 280 mm. long, the muscle is 29 mm. wide and 3.3 mm. thick where shown proximally transected in Figures 6-9, some 25 mm. below the origin. Below this point, it gradually narrows to its minimum width of 21 mm. (and thickness of 4.1 mm.) at 140 mm. and then broadens slightly to a distal maximum of 24 mm. (and thickness of 2.9 mm.) at 220 mm. A central strand of tendon becomes visible on the superficial surface at approximately 110 mm. and gradually widens as it proceeds distally, while shifting toward the radial border of the muscle. Contrary to the description of Beddard (1893, p. 189), the central cord of tendon also becomes visible on the deep surface (although covered by thin fascia) 5 mm. distal to its appearance superficially. On the deep surface, the tendon of insertion attains the radial border of the muscle from 93 to 43 mm. above the insertion, for a maximum surface width of 2.5 mm.; for most of the 43 mm. above the insertion, the tendon is entirely underlain by a radialward expansion of the belly on the deep surface (Fig. 6). The fleshy portion of the muscle reappears along the radial border of the tendon from 30 to 6 mm. above the insertion superficially, with a maximum width of 3.5 mm. (Fig. 4). The fleshy portion extends to within 5 mm. of the pisiform bone insertion on the ulnar border, and even nearer on the deep surface. As depicted in Figure 5 by the non-excised segment 75 to 80 mm. above the insertion, most of the distal third of the muscle is affixed to the ulna by moderately thin fascia extending from its dorsomedial border over the bone.

Section Q-R in Figure 16 shows the appearance of the muscle at the proximal transection, where it is 30 mm. wide and has a maximum thickness of 3.3 mm., while S-T depicts the distal section, 22 x 45 mm. (with the tendon 9.7 x 2.8 mm.). At its insertion on the pisiform bone, the tendon is 12.5 mm. wide. Upon excision some two years after death, the major portion of the muscle (between transections) weighed 21.1 gm.

The description of the origin of flexor carpi ulnaris provided by Sonntag (1923, p. 348) -- "by a narrow head from the internal condyle, by an expanded head from both internal condyle and olecranon, and by fascia from the upper fourth of the shaft of the ulna" -- seems more consistent with present observations than those of Beddard, previously cited. Sonntag's observation of the large size of the chimpanzee flexor carpi ulnaris relative to man's also conforms to the present specimen. The appearance of this muscle in the gorilla seems quite similar to that in the chimpanzee (Raven, 1950, p. 44). Fairly close similarity to the present chimpanzee flexor carpi ulnaris, the only major muscle of the ulnar sector of the antebrachial superficial flexors (Straus, 1942, pp. 292-294), is manifested by man and even by the much less closely related marmosets (Hill, 1957, pp. 150-151).

B. Deep Flexors

Flexor pollicis longus. In the deep (antebrachio-manual) flexor layer of musculature, the most radial representative is this large, flexor of the thumb, at the level of and extending parallel to flexor digitorum profundus (Figs. 8 and 9). Its origin from much of the anterior surface of the radius extends as high (on the ulnar surface of the radius) as 205 mm. above the tip of the radial styloid process, 5 mm. distal to the insertion of biceps (Fig. 10). The origin's superoradial border parallels the distal border of the supinator, with the intervening zone, 4-11 mm. wide, occupied by the insertion of pronator teres. In the proximal half of this zone, a few of the fascicles also arise from the tendon of insertion of pronator teres (also shared with flexor carpi radialis) near its attachment to the bone, and many arise from the overlying septum, as noted by Beddard (1893, p. 189).

In anterior view, its broad (to 11 mm. when measured with the adjacent muscle pulled away) superficial tendon of insertion, on the ulnar side, begins at 79 mm. from the proximal end of flexor pollicis longus and receives fascicles paralleling the tendon at this end but converging at 10 degrees only some 10 mm. farther down and gradually increasing (when relaxed) to 34 degrees near the wrist (Fig. 9). The muscle appears to be unipennate until the large proportion of shorter fascicles arising very deeply from the thick interosseus membrane are observed to enter the ulnar border of the tendon (unexposed in Figure 9) at angles somewhat smaller than on the radial side; thus the muscle is actually bipennate, despite the bilateral asymmetry.

It might be anticipated that the chimpanzee flexor of the thumb would be relatively smaller than in man because of the proportionately appreciably smaller thumb of the ape, as might seem somewhat corroborated by the lack (as in many humans) of a humeral head from the medial

epicondyle.[1] But contrary to expectation, this muscle is (like most chimpanzee muscles, however) decidedly thicker (to 24 x 16 mm.) and extends fleshily much further into the wrist area (9 mm. wide only 20 mm. above the end of the radial styloid process). Near the wrist, its angles of obliquity, elsewhere similar to man's, become perhaps slightly greater, thereby imparting more force without decreasing mobility (Edwards, 1965c). The explanation of the observed muscular size and form is not primarily that of an evolutionary compromise between the frequent need for a strong, opposable thumb and the equivalent pressure of brachiation toward thumb reduction. The explanation is instead to be found in the different functions compared to man; instead of primarily serving to flex the pollex, the major function in the chimpanzee is flexion of the index finger.

The complete separation of flexor pollicis longus from flexor digitorum profundus in this specimen was less marked in Chapman's chimpanzee (1879, p. 55). Champneys (1871, pp. 186-187), Beddard (1893, pp. 189-190), Sonntag (1923, p. 350), and Fick (1925, p. 124) have all reported two tendons for this muscle, the much larger one acting upon the index finger and the smaller upon the thumb; a comparable split in the tendon would presumably appear upon more distal dissection of the present specimen.

Flexor digitorum profundus. This broad, thick muscle, which lies beneath flexor sublimis and flexor carpi ulnaris except where it reaches the surface ulnarly (Figs. 3-10), is roughly 75 per cent heavier than its paralleling counterpart, flexor pollicis longus. Arising proximally from the anterodistal portion of the olecranon process, it lies just beneath and extends dorsally very slightly beyond the origin of flexor carpi ulnaris and dorsomedially alongside the deep head of flexor digitorum sublimis. Most of its origin is derived from the upper 60 per cent (to 165 mm. below the proximal end of the muscle) of the volar aspect of the ulna, to the mid-line of the medial aspect. Also observable are abundant accessory origins from the interosseus membrane and from the intermuscular septum superficial to the muscle; the last origin is what is likely referred to by Sonntag, who reported that "some of the fibres fuse with the flexor sublimis and flexor carpi radialis" (1923, p. 350).

At distances of 102, 142, and 153 mm. below the proximal end, tendons appear to anterior view from the radial to the ulnar side; more distally, these tendons manifest maximum widths of 11, 2.5, and 5 mm. respectively. The uppermost 27 mm. of the median tendon is hidden by a fold of several ulnar head muscle bundles after the entire muscle is exposed to anterior view (Fig. 9). Bipennate when all three heads are considered as a single unit, but with higher angularity on the radial side (roughly 20 degrees versus 15 degrees on the ulnar side, thereby not mirror-imaging flexor

[1] Interestingly, such humeral heads appear to have been derived from the intermediate sector of the superficial series (Straus, 1942).

pollicis longus), fleshy portions of the radial and ulnar heads extend to within only 48 and 36 mm. respectively of the ulnar styloid process tip, and less than 20 mm. deeply. Flexor digitorum profundus thus manifests a much greater contrast to the condition in man in respect to fleshy extension distally than does its more radial counterpart. At 23 mm. above the end of the ulnar styloid process, the radial, median, and ulnar tendons reveal dimensions of 5.8 x 3.9, 5.5 x 2.4 (composite dimensions for the median head's three tendons, which become fairly markedly separate for the distalmost 50 mm. above the styloid process tip), and 3.9 x 1.3 mm. respectively.

Champneys (1872, p. 186) has noted the lack of a tendon to the index finger from flexor digitorum profundus in his chimpanzee, as would have been anticipated if this digit is supplied by the other deep flexor and this muscle is limited to three tendons. Although Fick (1925, p. 124) has stated that the orangutan manifests the same separation in form and function for the two deep flexors as the chimpanzee and indicates that this separation applies to apes generally, von Bischoff (1880, p. 13) reported for his gorilla detailed descriptions of the tendons from a flexor digitorum profundus arising from both the ulna and the radius, while there was "no trace of a flexor pollicis longus." The lack of separation of the two muscles is presumably an individual anomaly, although perhaps reflecting an atavistic survival of the simgle deep flexor found in most other mammals, including the tree shrew _Tupaia_ (Straus, 1942, p. 298), but not the platyrrhine Hapalidae (Hill, 1957, p. 151).

Pronator quadratus. This is a relatively thin, flat, quadrilateral muscle in the distal fifth of the antebrachium which passes deep to all distal muscle bellies and tendons of the flexor group from its rather fleshy origin on the volar surface of the ulna to its even more fleshy insertion on the volar surface of the radius (Fig. 9). The fascicles arise 58 to 29 mm. above the tip of the ulnar styloid process, extend radiodistally approximately 30 degrees from the transverse direction, and insert 36 to 10 mm. above the distal end of the radius.

Sonntag (1923, p. 350) has recorded that the muscle extends from "the lower inch and a half . . . of the shaft of the ulna to the lower inch . . . of the shaft of the radius."

C. Superficial Extensors and Supinators

Brachioradialis. This long, flat muscle, the most proximal of a group of three muscles of parallel alignment in their major axes and their fibers, arises from the epicondylar ridge 136 to 60 mm. above the end of the 324.5-mm. humerus, which is 58.1 to 81.5 per cent down the length of the humerus. Since the leverage of brachioradialis is significant to an understanding of its form, it may be more consequential to note that the distance

from the center of rotation of the shoulder-joint to the axis of rotation of the elbow-joint is approximately 292 mm., while that from the elbow-joint to the wrist's axis of rotation is some 270 mm. The distance of the origin above the elbow-joint axis on the lateral side is roughly 126 to 50 mm., which is some 56.8 to 82.9 per cent down the length of the humerus between the centers of rotation. The muscle extends along the radial border of the volar aspect of the forearm and inserts broadly upon the proximal portion of the radial styloid process some 400 mm. from the muscle's proximal end when extended (Figs. 2-15). It is fairly uniformly 26 mm. wide and of 8 mm. maximum thickness from near the origin to the central portion. It begins to fuse to a central tendon on the deep surface 145 mm. above the styloid process tip, and rather abruptly across the entire muscle to a broad, thick tendon at 105 mm. above the tip of the radius on the superficial surface (Fig. 15). The tendon of insertion narrows to 6 mm. and thickens to some 1.5 mm. before attaching to the bone.

The present writer has very recently provided a little comparative study of the form and function of this muscle in a few primates (Edwards, 1965c).

Extensor carpi radialis longus. Although this muscle is not at all covered by brachioradialis at its origin -- from the distal portion of the humerus and, like brachioradialis, from the heavy, wide lateral intermuscular septum -- between the middle of the anterior border of the tendon overlying the lateral epicondyle of the humerus to a point 43 mm. more proximal, it parallels the larger muscle down the radial border of the forearm under progressively greater cover of brachioradialis until it is completely obscured superficially (dorsally) above the mid-point of its total length -- at which point it is also covered deeply by extensor carpi radialis brevis (Figs. 9-15). Its relatively small tendon of insertion has dimensions of 4.5 x 1.3 mm. as it enters the wrist to insert upon the base of the second metacarpal. Extensor carpi radialis longus averages approximately one-fourth as massive as brachioradialis, and roughly two-fifths as large as extensor carpi radialis brevis, despite the much slimmer origin of the latter.

Beddard (1893, p. 187) has reported that in his chimpanzee extensor carpi radialis longus was "short, not reaching halfway down the forearm"-- a condition more extreme than the distal attenuation in the present specimen.

Extensor carpi radialis brevis. Unlike the other two muscles in the group which have broad origins, at its proximal end this muscle is only some 3 mm. wide, wedged between extensor carpi radialis longus and extensor digitorum communis (Figs. 9-15). But it quickly expands to intermediate size (to a maximum of 21 x 5 mm.) before it enters the wrist by a tendon (dimensionally 5.5 x 2.0 mm.) to insert upon the base of the third metacarpal.

The chimpanzee studied by Beddard (1893, p. 188) displayed no fleshy portion to this muscle beyond 6 inches below the proximal end and 2 inches below the end of its fusion with extensor digitorum communis, in marked distinction with the present specimen. Fick (1925, p. 125) has reported that in his later chimpanzee, in contrast with extensor carpi radialis longus, this muscle is pennate, which is to some degree the form of the present specimen -- as is not unexpectable in view of the contrasting broad and narrow origins of the two muscles (Fig. 15).

As generalized by Hill (1955, p. 41), all three of the muscles in the foregoing group conform to the fairly precisely limited pattern characteristic of all haplorhines (the tarsier and all "higher" primates); among all primates, the radial extensors are "essentially conservative" (Straus, 1941, p. 41).

Extensor digitorum communis. This is another broad, flat, superficial muscle -- quite similar to brachioradialis in general form and especially dimensions -- which occupies much of the extensor surface of the forearm (Figs. 11-15). At its proximal end, extensor digitorum communis arises from part of the common tendon-sheet of origin extending from the lateral epicondyle of the humerus (Fig. 13). From a narrow, thin belly only 11 x 3 mm. at 35 mm. from its proximal end, this muscle broadens to maximum dimensions of 26 x 5.5 mm. at approximately its belly's mid-point. A tendinous septum, from which both sharing muscles take extensive origin, occupies its zone of contact with extensor carpi radialis brevis along the proximal half of the muscle. This tendon-septum -- continuous with the moderately large area of superficial tendon on the radial side of the muscle immediately below its mid-point (Fig. 13) -- extends some 5 mm. almost perpendicularly (but somewhat radially) from the dermis and then extends radially, underlying extensor carpi radialis brevis, almost parallel to the dermis. This septum not only provides apparently the primary area of origin for the muscle underlain by it but also, from its smaller, perpendicular portion, a significant part of the origin of the common extensor here described. From a somewhat comparable septum on the ulnar side arises a large proportion of the fleshy bundles converging moderately obliquely with the radial bundles at the approximate mid-line of the muscle. Extensor digitorum communis also takes origin from the very thick antebrachial fascia (Fig. 12), as do the two extensors ulnar to it.

The fleshy portion of this parallel-pennate to bipennate muscle manifests a central line of fiber convergence which both superficially and deeply extends from the radial border near the proximal end to the approximate mid-line slightly below the middle of the belly. The muscle narrows until it fuses to four tendons, which are bound closely together by thin fascia, as is the case elsewhere in the wrist area for groups of

related tendons. The majority of the fascicles in the proximal half of the belly of the combined muscle fuse to the heavy median tendon, while most of the fascicles in the distal half fuse to the slimmer tendons on either side, with allocation to radial and ulnar tendons consistent with the dual division evident both superficially and deeply (Figs. 13-15). The tendon along the radial border extends highest to superficial view; it appears deeply at 75 mm. above the tip of the ulnar styloid process, while the distalmost tip of its associated fleshy portion extends to 41 mm. above. The tendon of the median segment appears deeply (on the combined muscle) at 120 mm. above the distal tip of the ulna, but when the segments of the muscle are separated it is seen to extend appreciably higher, while its belly extends to 14 mm. above. Under cover of a fleshy fold of the ulnar segment, the median tendon appears to superficial view only as high as 8 mm. above the ulnar tip, and is partially covered by this fold to 4 mm. below the tip. The two-fold, narrow ulnar tendon, with superficial and deep branches of equivalent size, appears deeply at 16 mm. above, while the fleshy portion (superficial and overlapping the median segment radially) extends to 4 mm. below the ulnar styloid process. At 4 mm. below the tip of the ulnar styloid process, the radial to ulnar tendons are respectively 3.0 x 1.4 mm., 4.3 x 1.4 mm., and 3.0 x 1.7 mm. (the third measured as a single unit but presumably two tendons extending separately to digits IV and V). The tendons of the muscle traverse the wrist at approximately the center-line.

Champneys (1872, p. 183) indicated that in his chimpanzee there was no separation of this muscle from the adjacent extensors until a third of the muscle's length had been traversed. In the present specimen, although the fascicles are fused to the intermuscular septa, the separations are very clear. Likely the apparent inconsistency here is merely semantic, however. In the gorilla (Raven, 1950, pp. 46-47) and in man, the general form of this muscle is very similar to that described. In various higher primates, the superficial extensor, somewhat variable in man, may terminate in three (Leontocebus), four (Macaca), or five (Hapale) tendons (Hill, 1955, p. 41).

Extensor digiti quinti (or minimi) proprius. Closely contiguous and ulnar to the longer and much more massive extensor digitorum communis and quite similar to its form in man, this muscle is separated only by a thick tendinous septum -- from which, as well as the antebrachial fascia, it arises -- from its proximal end 172 mm. above the tip of the ulna to a point only 65 mm. above the ulnar tip, for a short distance below which contact with the larger muscle is maintained by thin fascia (Figs. 13-15). The tendon-septum also extends ulnarly -- without, however, closely approaching the ulna -- beneath this small extensor and, along with the antebrachial fascia, provides origin for the muscle throughout the length of the tendon-septum. The muscle expands to maximum dimensions of 10 x 2.9 mm. in the middle of its antebrachial sector. The tendon of insertion appears near the ulnar border 40 mm. above the ulnar tip. As it traverses the wrist beneath the dorsal carpal ligament, this organ measures 3.5 x 1.4 mm. at the level of the ulnar tip, of which only 1.2 x 1.4 mm. is tendon; oddly by human standards, the belly extends more than 25 mm. beyond the ulnar tip.

Extensor digiti quinti proprius was apparently "totally absent" in another chimpanzee specimen, unless it was misidentified as part of extensor digitorum communis (Beddard, 1893, p. 188). A second origin of extensor digiti quinti proprius from the ulna has been found in individual humans, gibbons, and *Cebus*, and the ulnar head alone has been reported as an anomaly in macaques, orangutans, and chimpanzees (Straus, 1941, p. 49).

Extensor carpi ulnaris. Also arising from the common extensor tendon of the lateral epicondyle -- as well as from the underlying septum, the overlying fascia, and to some extent from the muscle's narrow zone of contiguity with the dorsoradial surface of the ulna -- this muscle maintains fairly constant dimensions approximating 19 x 3.5 mm. over most of its fleshy length (Figs. 13-15). Tendon of insertion appears on its radial border 115 mm. proximal to the tip of the ulna and broadens to cover most of the width at 75 mm. above this tip. Yet the fleshy strip continues along the ulnar border of the tendon to within only 35 mm. of the ulnar tip; at the distal tip of the belly, the tendon manifests dimensions of 3.9 x 2.3 mm.

The lack of a second (ulnar) head of origin of extensor carpi ulnaris is a primitive trait, shared with many but not all primates (Straus, 1941, p. 48).

D. Deep Dorsal Muscles

Most of the deep muscles of the forearm's extensor surface appear to have evolved through migration of origins up from the hand, just as the superficial muscles have tended to migrate distally (Straus, 1941).

Supinator. Except for somewhat more extensive development, this flat, rhomboid-shaped muscle is similar to that of man; the area of tendinous origin on the lateral epicondyle of the humerus and the supinator crest of the ulna is covered by the superficial extensors (Fig. 15). The fascicles extend obliquely distalward and radially to curve around the dorsoradial and volar surfaces of the proximal 120 mm. (42.4 per cent) of the radius,[2] upon which it inserts fleshily along the superolateral border of the oblique line proximally to the border of the biceps tendon for a total length of 76 mm., from slightly ulnar to the mid-volar surface to the mid-radial (mid-lateral) surface of the radius (Figs. 9 and 10).

Chapman (1879, p. 55) has commented that on his chimpanzee "the supinator longus arose from the humerus much higher up than in Man." In the

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[2]As measured radiographically, the humerus of the present specimen is 324.5 mm. in length, while the lengths of the radius and ulna are 283.0 and 301.5 mm. respectively. In anteroposterior view, the radius and ulna are 11.5 and 12.8 mm. in diameter at their mid-points, where they are separated by a 26-mm. hiatus; laterally, they are at their mid-points 13.5 and 11.5 mm. in diameter respectively. Additional panometric data are presented in the companion paper (Edwards, 1965*a*).

specimen of Beddard (1893, p. 188), as in his orangutan, the muscle here considered was described as "distinctly double," as almost an inch thick, and as inserting "on to the radius for more than one third of its length." Parsons (1898, pp. 735-736) has provided comparative data on this muscle in other mammals.

Abductor pollicis longus and "extensor pollicis brevis." Abductor pollicis longus is quite thoroughly fused with "extensor pollicis brevis" to form that which is in essence a flat, fusiform, bipennate muscle occupying the radial two-thirds of the deep extensor layer of the distal 60 per cent of the forearm; it also extends farther to the ulnar side along the second fifth (reckoning proximally to distally) of the length of the ulna, where it attaches to this bone (Figs. 13-15). This is not a typically bipennate muscle, however, in that only thin fascia rather than tendon forms the median line of junction, at least superficially. The origin of this composite muscle (as the writer would in this specimen regard it) is from the third seventh (76 to 114 mm. from the proximal end of the 301.5-mm. ulna) of the radial surface of the ulna, from the interosseus ligament (membrane), from the mid-radial (for 67 mm. immediately distal to the supinator) to ulnar aspects of the third quarter of the shaft of the radius, and to a moderately marked extent from the septa which separate it from the overlying superficial extensors (Fig. 15). The most distal 28-mm.-long portion of the mid-line of the belly is less tightly fused than more proximally. On the ulnar side the fleshy portion extends 10 mm. farther, before fusing to a second tendon (of "extensor pollicis brevis"), which proceeds into the wrist tightly adjacent to the radial tendon. The belly of the muscle varies from 27 to 30 mm. in width over most of its length. The abductor and extensor tendons are of almost identical size, 6.8 and 6.5 mm. in width at the distal ends of their respective fleshy portions and constricting to 5.2 and 5.0 mm. wide at the most distal extent shown in Figure 15, where they are 1.7 mm. thick.

Champneys interpreted his chimpanzee specimen to have "two quite separate bellies" of extensor ossis metacarpi pollicis, as well as an abductor pollicis, but to have been missing extensor pollicis brevis (1871, p. 184); likely these two bellies and their separate tendons refer to the composite muscle here described. On the other hand, Beddard's (1893, p. 188-189) description conforms closely to that of Champneys, and it notes another "hardly separable" extensor ossis metacarpi pollicis (extensor pollicis brevis) superficial to it as well. In Sonntag's specimen (1923, p. 352) the two quite closely resembled the muscles here described, except for the difference in tendon size, with "a common origin from the bones of the forearm . . . . The tendons separate from the combined muscular mass. The broad tendon of the former [extensor ossis metacarpi pollicis] runs to the trapezium and thumb sesamoid, and the slender tendon of the latter goes to the base of the metacarpal of the thumb." Fick (1925, pp. 125-126) has provided a description of abductor pollicis longus similar to the others just noted, but with the observation that it was bipennate. In the same paper, he reported that extensor pollicis brevis was also bipennate in this chimpanzee, but almost completely

covered by abductor pollicis longus, although in an earlier specimen (1895, p. 299) the short muscle was "not present," while the abductor inserted with two tendons.

Straus has discussed at length the variation in form of these two muscles. He interprets the "extensor pollicis brevis" ("extensor primi internodii pollicis") attaching to the pollical metacarpal bone as probably not homologous to the extensor pollicis brevis of man but derived from abductor pollicis longus, and thus misnamed. Straus would restrict "extensor pollicis brevis" to muscles inserting on the phalangeal portion of the thumb, and thus, among all mammals, restricted to man, the gorilla (9 of 16), and the gibbon (1 of 15). Hill (1955, p. 42) is in agreement with Straus, stating that extensor pollicis brevis "occurs only in Man and Gorilla." The tendon of the long abductor at least sent a slip, as in man, to the proximal pollical phalanx in 4 of 9 gorillas but in only 1 of 20 chimpanzees (Keith, 1899, pp. 305-306). It is interesting to observe that von Bischoff commented on this confusion in terminology many decades ago (1880, p. 14). Additional literature indicates part of the reason for the confusion in this area -- the fairly high variability, both intraspecifically and interspecifically, in these muscles of the first digit.

Extensor pollicis longus. The fleshy portion of this fusiform, essentially parallel muscle underlies extensor carpi ulnaris and, more ulnarly and distally, extensor indicis proprius; it overlies the most ulnar portion of "extensor pollicis brevis." The muscle arises in part superficially from the septum separating it from extensor carpi ulnaris, proximally from the thin septum (which thins rapidly beyond a point only 25 mm. distal to the muscle's proximal tip and does not significantly provide any origin distal to that point of thinning) separating it from the extensor pollicis brevis portion of the composite muscle described previously, and most importantly from the dorsal half of the radial aspect of the middle fifth (115 to 170 mm. distally of the 301.5-mm. bone) of the ulna immediately distal to the origin of the muscle previously considered (Fig. 15). The belly varies from 10 to 13 mm. in width and 1.5 to 2.7 mm. in thickness over most of its length. Although the distal portion of the belly of the muscle is very thin, it extends on the ulnar side of the tendon to a point only 35 mm. above the tip of the ulnar styloid process, although tendon appears superficially on the radial border 60 per cent of the way from the muscle's proximal end to the wrist. After extending beyond the fleshy portion, the tendon remains quite uniform dimensionally, and is 2.8 x 1.2 mm. in size as it enters the wrist. The tendon enters the wrist almost precisely at the mid-line between the ulna and the radius, and thus much more ulnar than the same muscle in man.

Extensor pollicis longus in the chimpanzee subject of Champneys (1871, p. 184) had, in addition to its insertion on the second phalanx, a slip to the first phalanx, as is often the case in man, but not in Chapman's chimpanzee (1879, p. 55); Champneys reported that this muscle arose from an area 2 to 2.5 inches long in the middle of the ulna -- almost twice as

long as on the present specimen. In Fick's later chimpanzee (1925, p. 126) it was "very weak."

Extensor indicis proprius. Arising from a 57-mm.-long area (171 to 228 mm.) of the radial aspect of the ulna immediately distal to the area of origin of extensor pollicis longus, and secondarily from the overlying septum, the belly of this muscle, very similar in form to extensor pollicis longus, is fairly intimately fused to that muscle in its proximal quarter, separated only by inconspicuous, thin fascia (Fig. 15). It is 9 to 12 mm. in width along most of the proximal 60 per cent of its fleshy portion. At its maximum width it is only 2.5 mm. thick, but, unlike extensor pollicis longus, it thickens markedly as it constricts in width more distally, and where its width has decreased to approximately half (6.5 mm.) at 16 mm. above the proximal end of the tendon exposed superficially, its thickness is more than doubled to 5.8 mm. The fleshy portion extends to within 9 mm. of the tip of the ulna on the ulnar side of the tendon and 2 mm. beyond the tip of the ulna on the other side. The tendon of insertion, 2.9 mm. wide and only 0.7 mm. thick at the distal end of the fleshy portion, constricts to 2.1 mm. at 12 mm. more distally.

The only significant difference in the extensor indicis proprius of Beddard's chimpanzee to that of the present specimen was that it originated also from the volar surface of the ulna (1893, p. 188). In a specimen of Fick, it is described as "very weak."

Instead of the primitive condition of separate deep extensors for each digit, the number of bellies and tendons is normally more limited in higher primates; man is unique in this reduction trend in customarily having only deep tendons to the thumb and index finger (Hill, 1955, p. 41). "The arrangement of muscles on the back of the hand, as in the case of those of the flexor aspect and of the thumb, is most primitive in the Chimpanzee. In both apes the superficial extensor muscle to the fifth finger is small or absent; the extensor indicis, a muscle of the deep layer of extensors, was present in all the Chimpanzees examined, but only in 7 out of 8 Gorillas; the deep extensor of the 3rd digit was present in none of the Gorillas, but in 5 of 12 Chimpanzees; the corresponding tendon to the 4th digit was present in 1 of 8 Gorillas and in 4 of 12 Chimpanzees. The deep extensor of the fifth digit was present with equal frequency" (Keith, 1899, p. 306).

Anconeus. This "distal extension of the lateral part of the triceps" of primates (Hill, 1955, p. 39), which aids triceps in extending the antebrachium and might thus have been better considered with the brachial musculature, arises as in man from the lateral epicondyle of the humerus and proceeds slightly ulnarly as it extends to insert upon the dorsal portion of the radial aspect of the proximal fourth of the ulna (Fig. 15). Beginning at the lower border of the olecranon process, the total length of insertion is 55 mm., from 18 to 73 mm. below the proximal tip of the ulna. The maximum width at the proximal end of this thin, flat, triangular muscle is 17 mm.

Most writers have described anconeus simply as being similar to the human muscle in the chimpanzee.

4. INTERPRETATIONS AND EVALUATION

Most of the musculature operating the hand is concentrated in the forearm, where greater massiveness for strength, and length for mobility, can be better afforded. Because the muscles of the forearm are in most cases quite long relative to the portion moved, they can afford a loss in mobility through bipennateness for the compensation of increased strength. Furthermore, pennate muscles derive greater strength from additional fleshy length; despite the advantage of the chimpanzee's markedly greater antebrachial length relative to trunk length or general body-size compared with man (Schultz, 1936), many of the chimpanzee bipennate muscles extend farther toward or into the wrist area than in man, at little expense in increased mass or decreased mobility. Compared with those of man, most of the antebrachial muscles are also relatively broad and thick -- again for increased strength of the pectoral limbs, which are emphasized in the semi-arboreal, brachiating chimpanzee. Further discussion of some of the musculature of the chimpanzee is provided in recent papers by the writer (1965a; 1965b; 1965c).

The present report has provided the most detailed verbal and graphic data published to date on the antebrachial musculature of the chimpanzee. But the study was necessarily limited to only one specimen. At the end of the companion paper (1965a) on the thoracic and brachial musculature of this specimen, a fairly recent statement of the need for an adequate sample of specimens was quoted. Much earlier, at the close of the nineteenth century, Keith (1899, p. 304) observed that "it is only by dealing with a large number of [chimpanzee specimens] that their essential characteristics can be arrived at." Earlier still, Brühl (1871) had noted that "in no department of anatomy more than that which treats of the muscles is it more essential that we should not decide whether a form is normal or exceptional until it has been repeatedly examined."

In final evaluation, then, it seems evident that a great deal of additional study of the antebrachial musculature of the chimpanzee is needed before it can be considered satisfactorily known and understood.

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APPENDIX

Figures 1 through 16

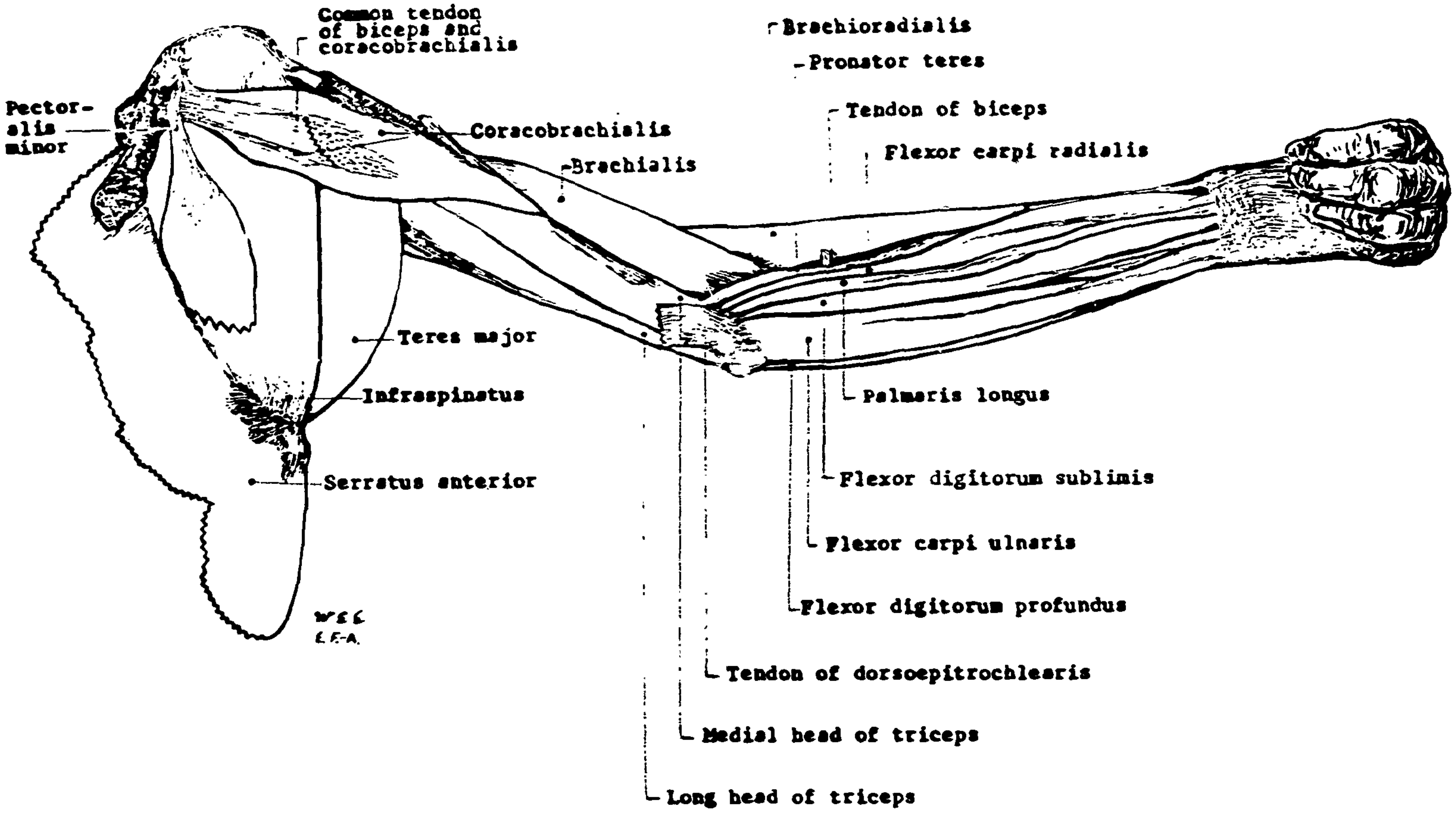

Figure 1

Anteromedial View of Scapular, Brachial, and Antebrachial Musculature With Deltoid, Biceps, and Dorsoepitrochlearis Removed

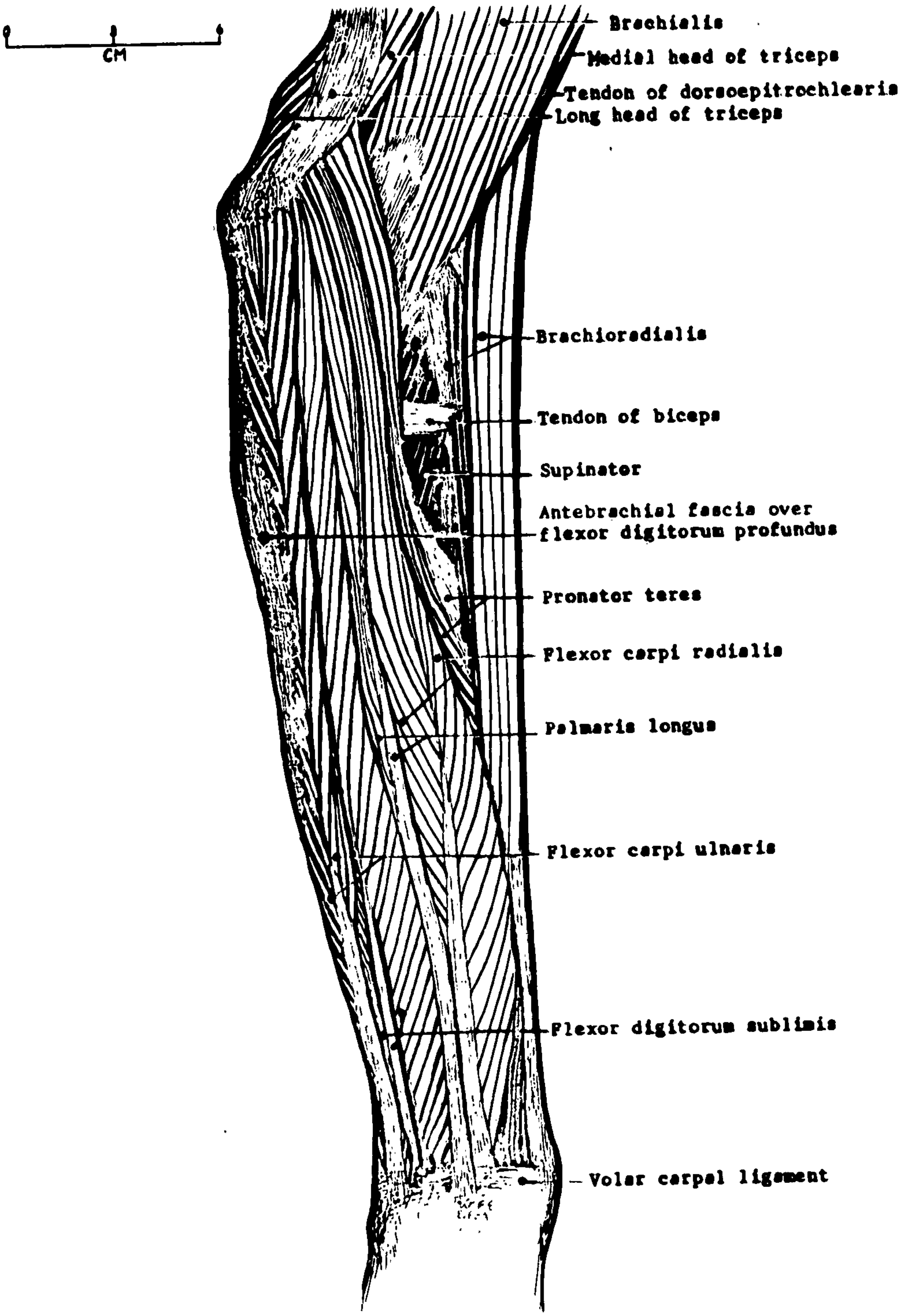

Figure 2

Flexor (Volar) Surface of Antebrachium, with Dermis Removed

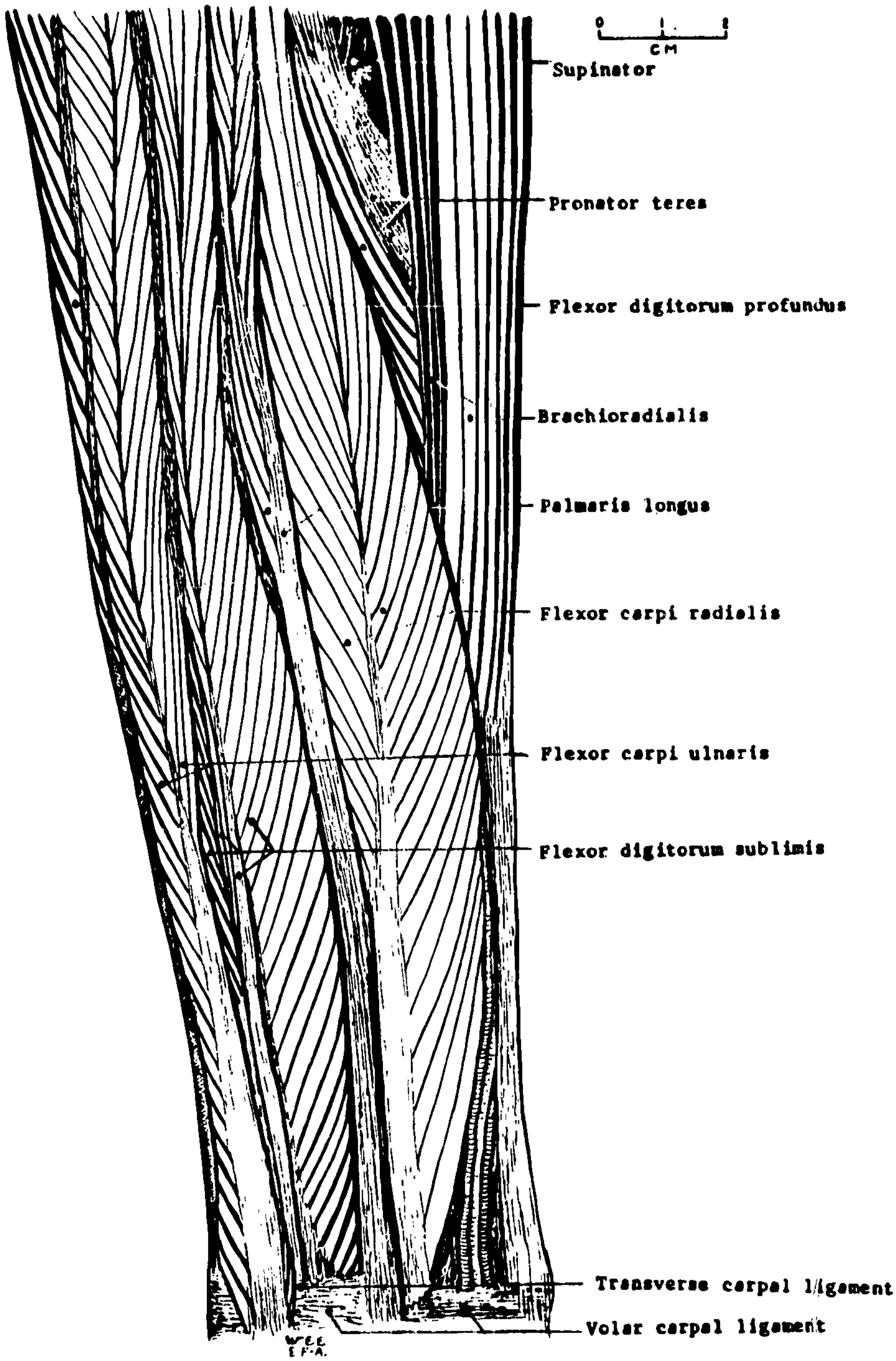

Figure 3

Flexor Surface of Distal Two-Thirds of Antebrachium, with Dermis Removed

Note that several narrow strips of antebrachial fascia, such as that between flexor carpi ulnaris and flexor digitorum profundus, remain, fused to the intermuscular septa underlying them.

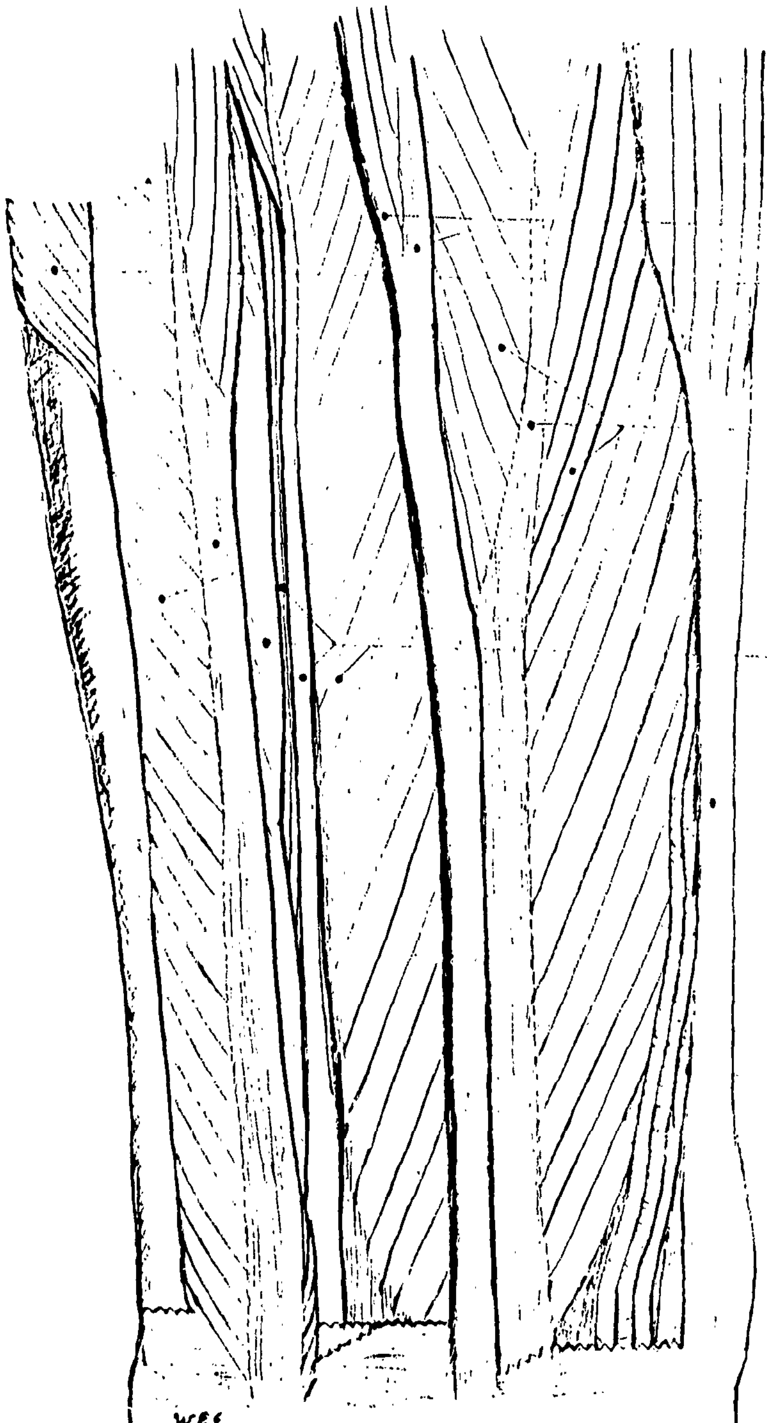

Figure 4

Enlarged View of Distal Portion of Flexor Surface of Antebrachium, with Dermis Removed

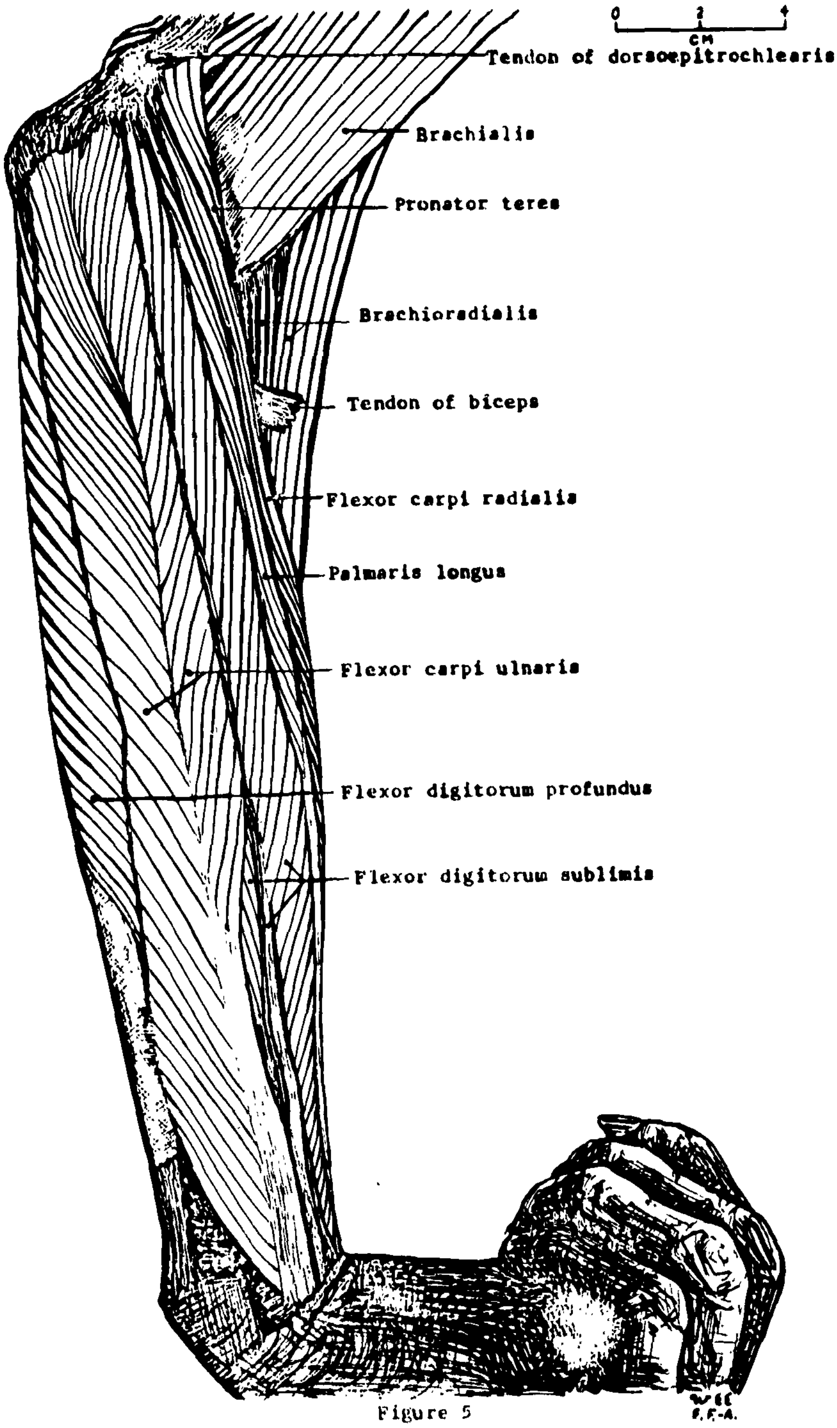

Figure 5

Medial View of Antebrachium, with Dermis Removed

Note the non-excised portion of fascia affixing flexor carpi ulnaris to the ulna some 75 to 80 mm. above the insertion of the muscle upon the pisiform bone.

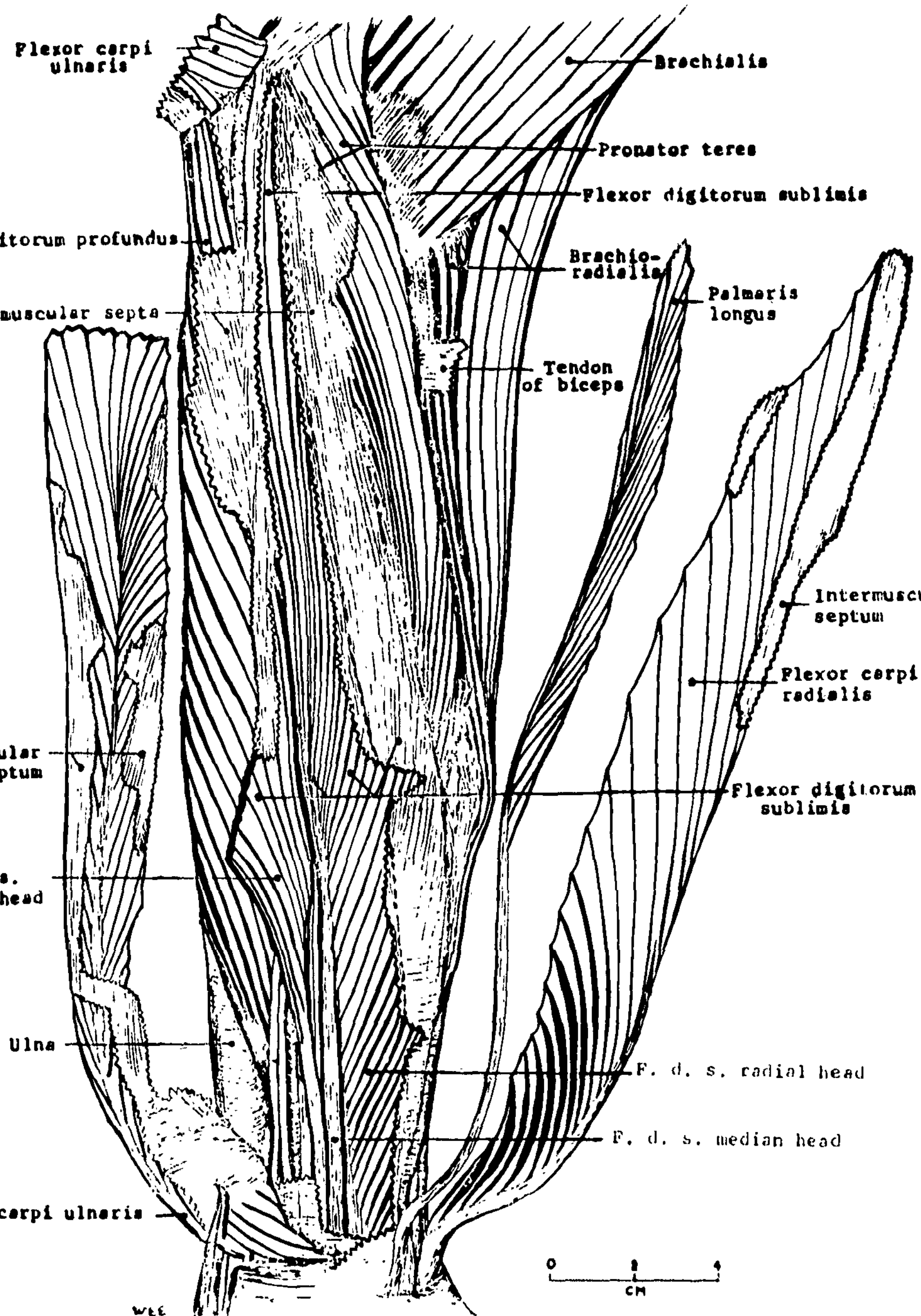

Figure 6

Anterior View of Antebrachium, with Flexor Carpi Ulnaris, Palmaris Longus, and Flexor Carpi Radialis Transected Proximally and Displaced to Show Their Deep Surfaces and the Underlying Structures

Serrated borders represent septa transections, generally rather arbitrarily located.

The dashed line indicates the line of contact between flexor carpi radialis and palmaris longus on the superficial surface of the intermuscular septum between these muscles and flexor digitorum sublimis.

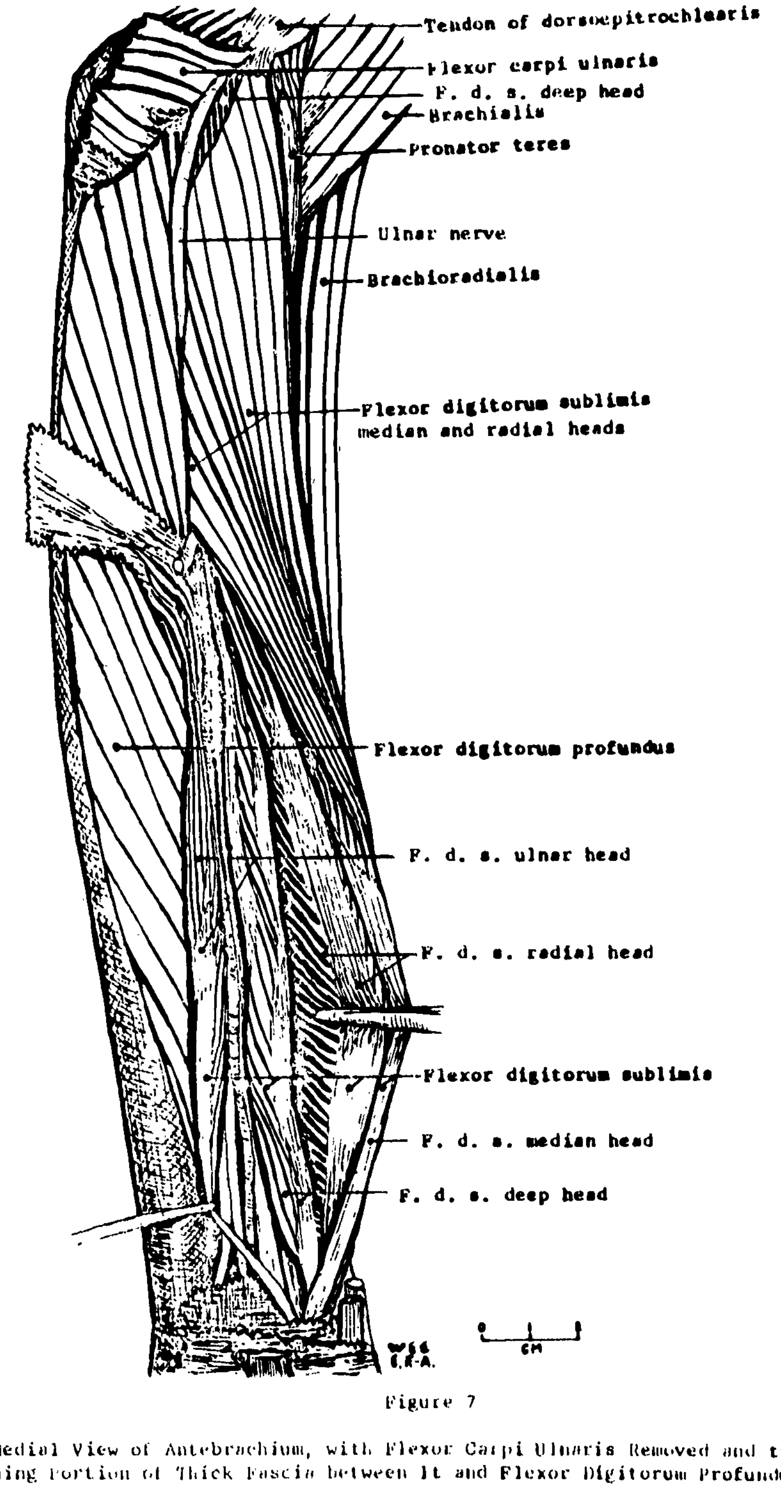

Figure 7

Medial View of Antebrachium, with Flexor Carpi Ulnaris Removed and the Small Remaining Portion of Thick Fascia between It and Flexor Digitorum Profundus Displaced

Note the small area of the deep head of flexor digitorum sublimis exposed at the muscle's proximal end.

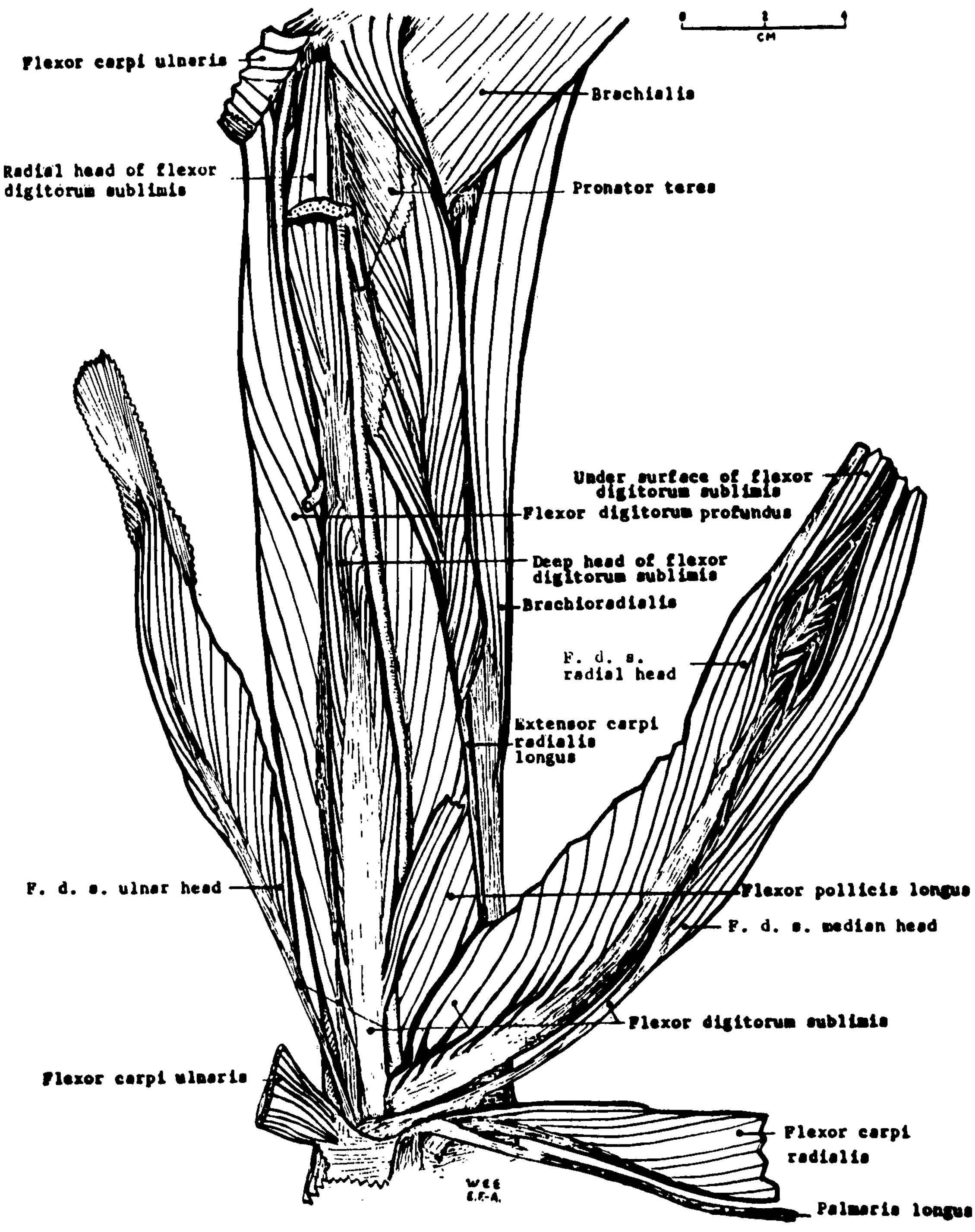

Figure 8

Anterior View of Antebrachium, with Ulnar, Median, and Radial Heads of Flexor Digitorum Sublimis Displaced to Show Their Deep Surfaces and the Structures Underlying these Muscles

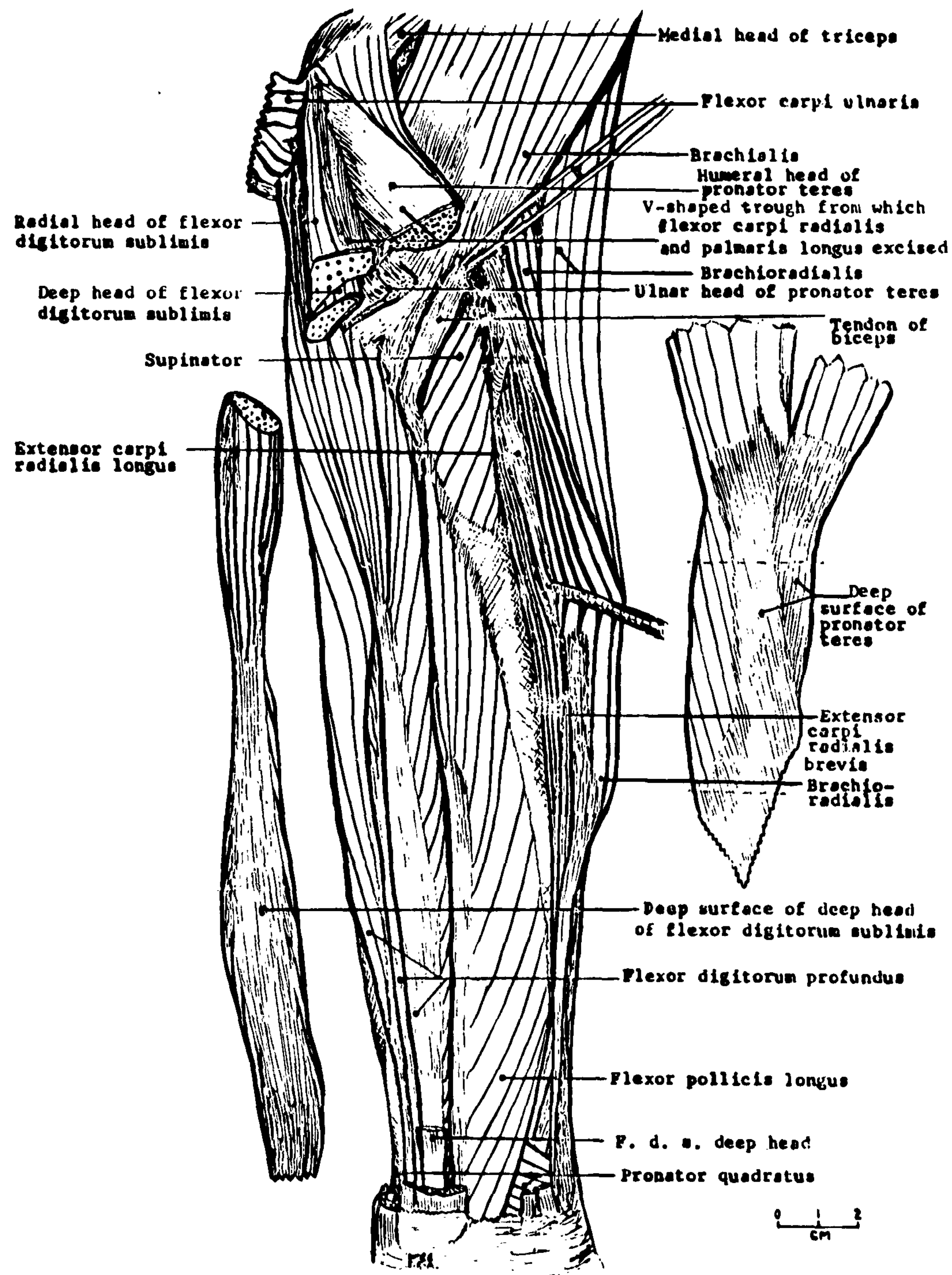

Figure 9

Deepest Layer of Antebrachial Flexors, with Pronator Teres and the Deep Head of Flexor Digitorum Sublimis Transected and Displaced to Show Their Deep Surfaces and Structures Underlying Them

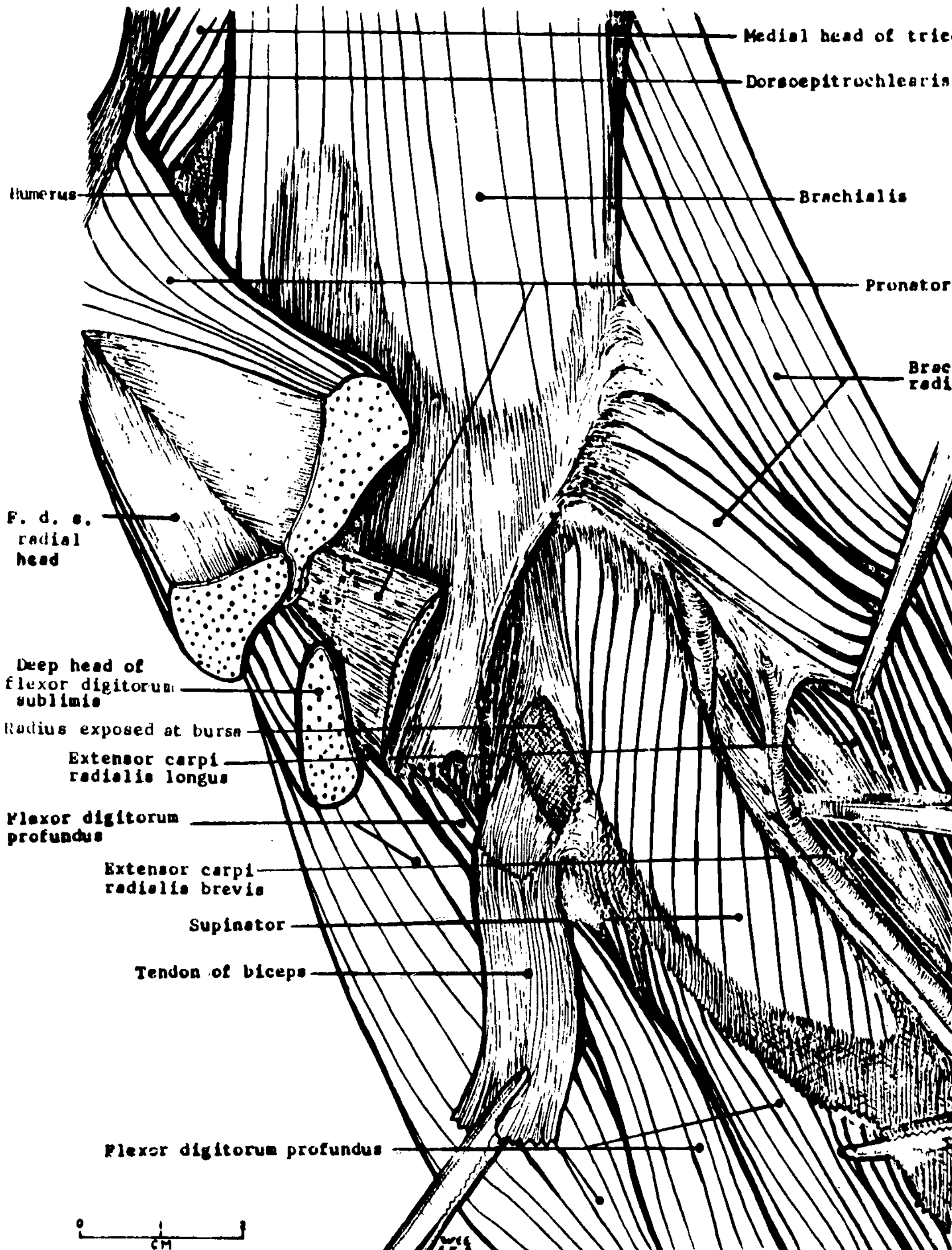

Figure 10

Enlarged Anterolateral View of Deepest Flexor Layer at Elbow
With the More Superficial Musculature Transected and Removed

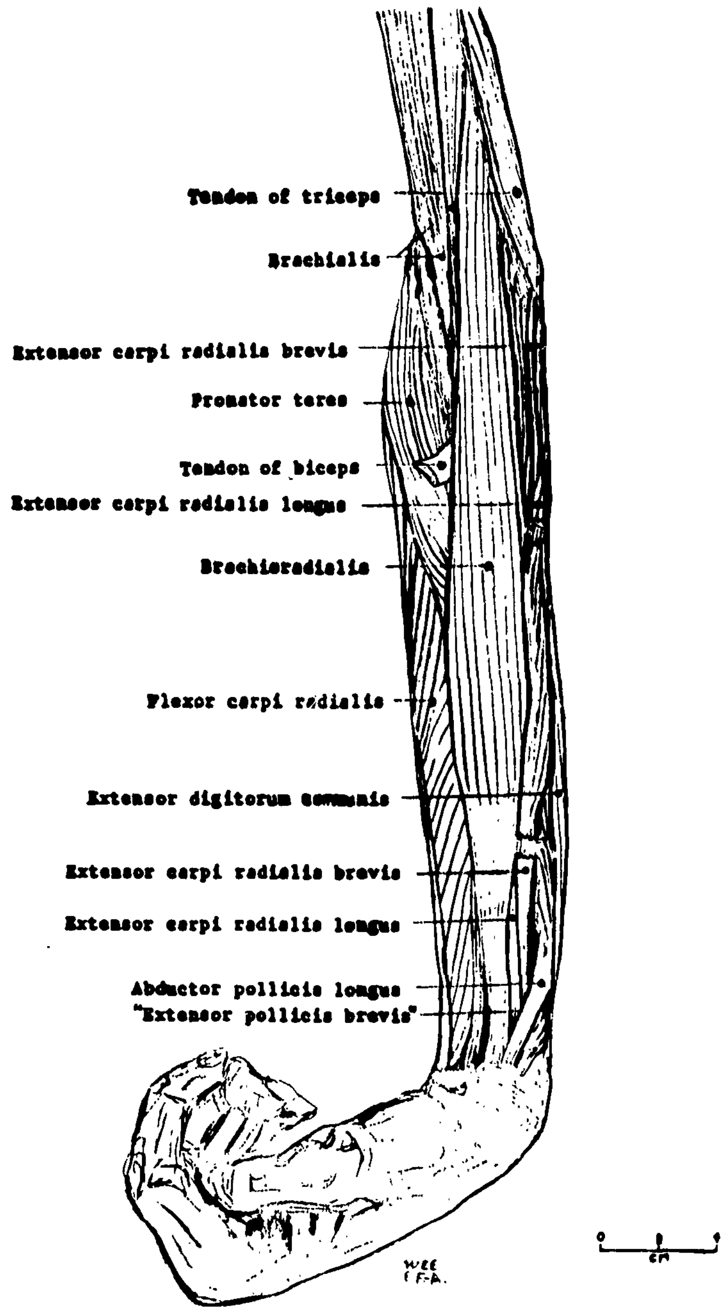

Figure 11

Lateral View of Antebrachium, with Dermis Removed

Note the two small fragments of dense antebrachial fascia (not removed in the above dissection) which bind brachioradialis to the more ulnar dorsal muscles; the two preserved fragments, some 200 and 90 mm. above the radial styloid process, extend from the dorsal border of brachioradialis to the septa between extensor carpi radialis brevis and extensor digitorum communis (at the proximal fragment) and abductor pollicis longus (at the distal fragment), as in Figure 13.

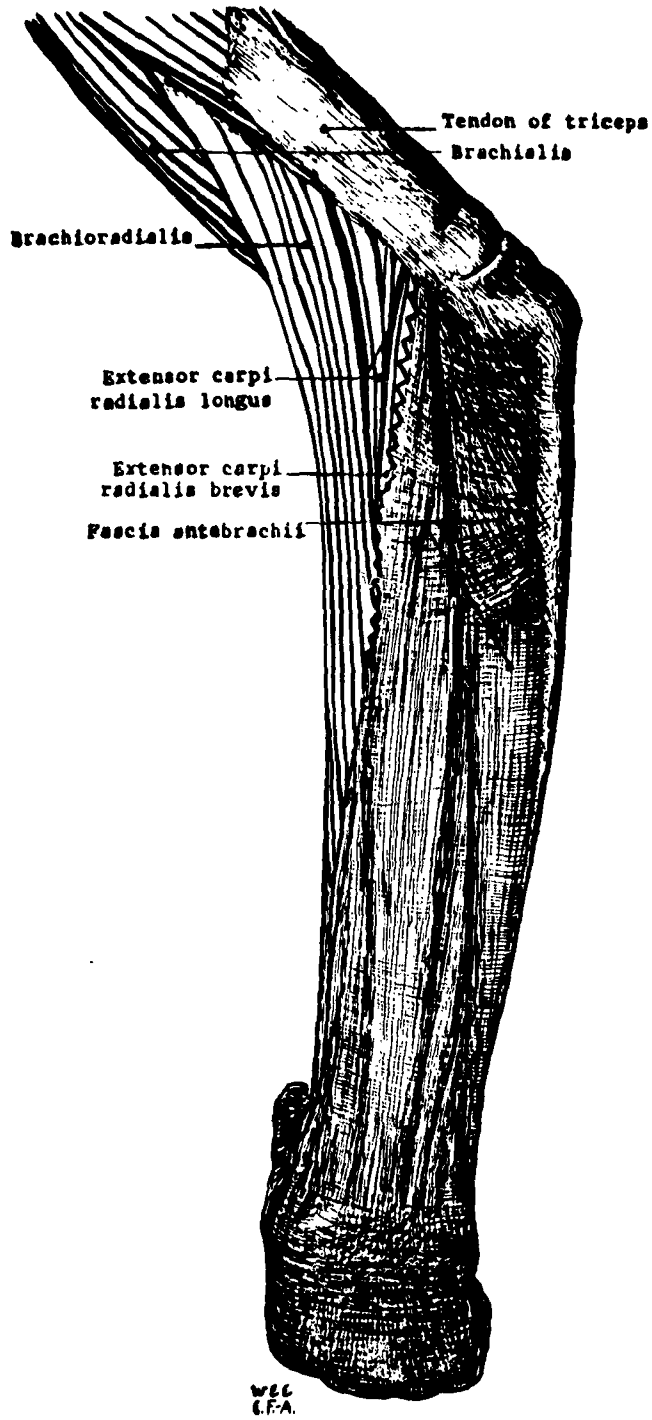

Figure 12

Extensor (Dorsal) Surface of Antebrachium
With Dermis Removed but Showing
All except Thinnest Antebrachial Fascia

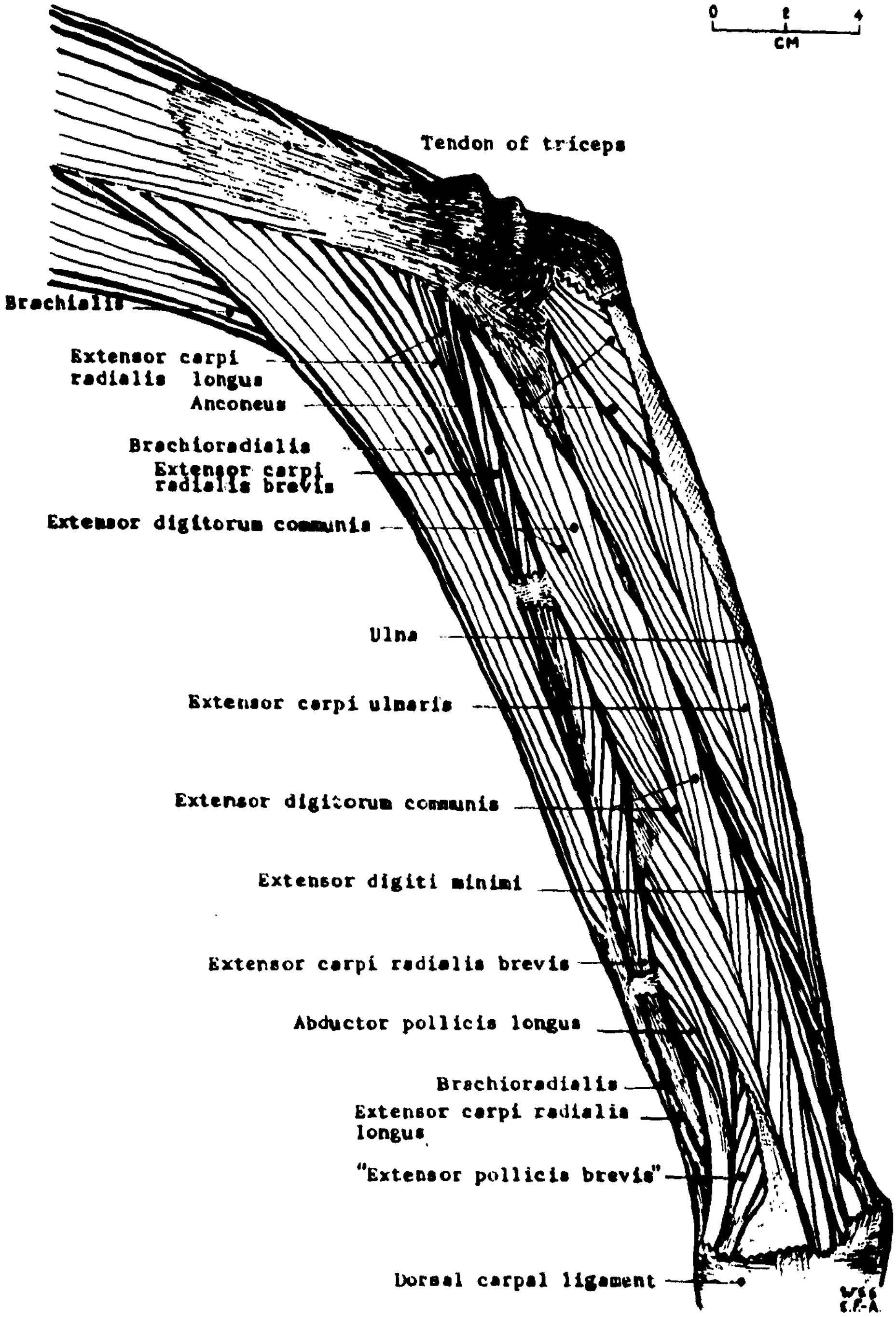

Figure 13

Extensor Surface of Antebrachium, with Fascia Removed

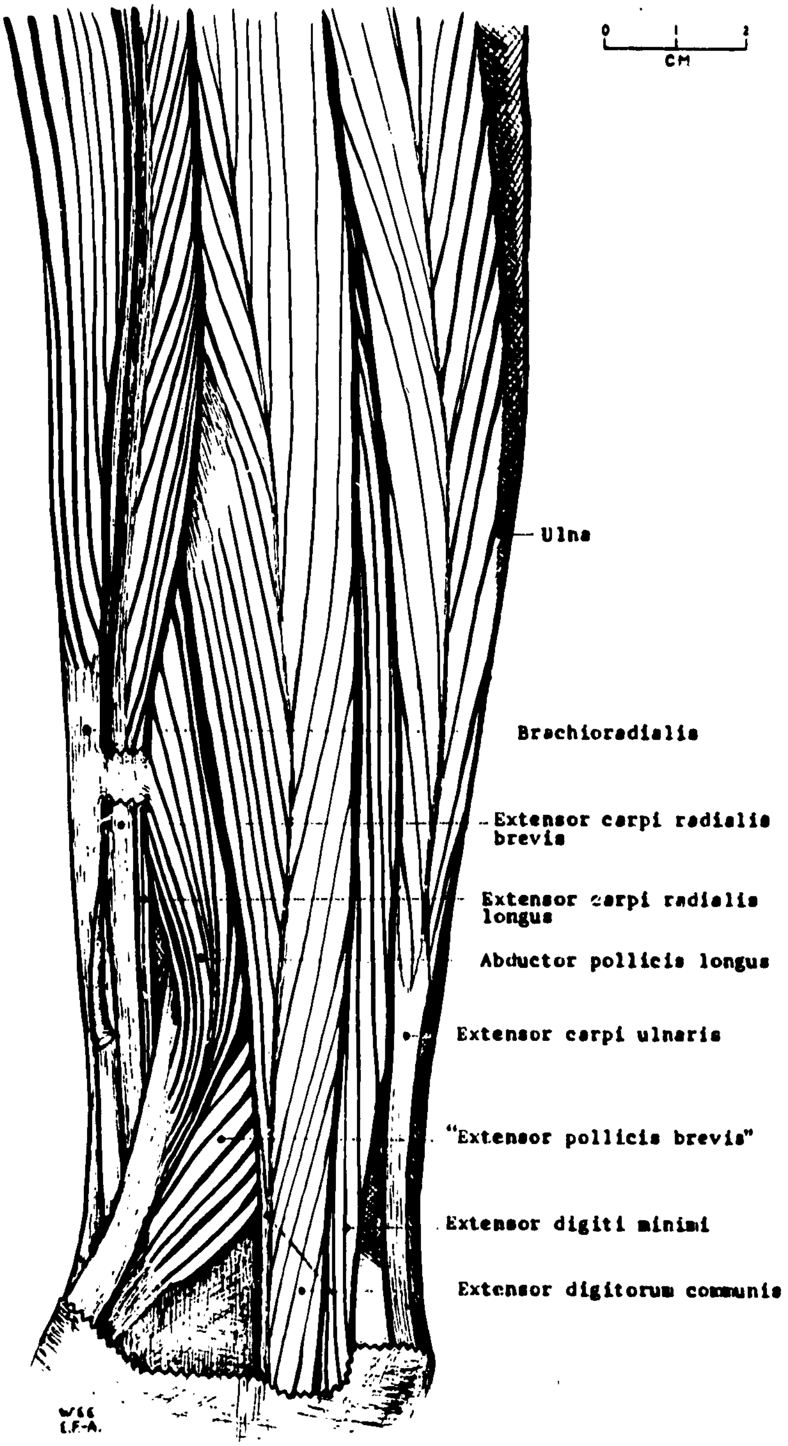

Figure 14

Enlarged View of Distal Portion of Dorsal Surface of Antebrachium, with Dermis Removed

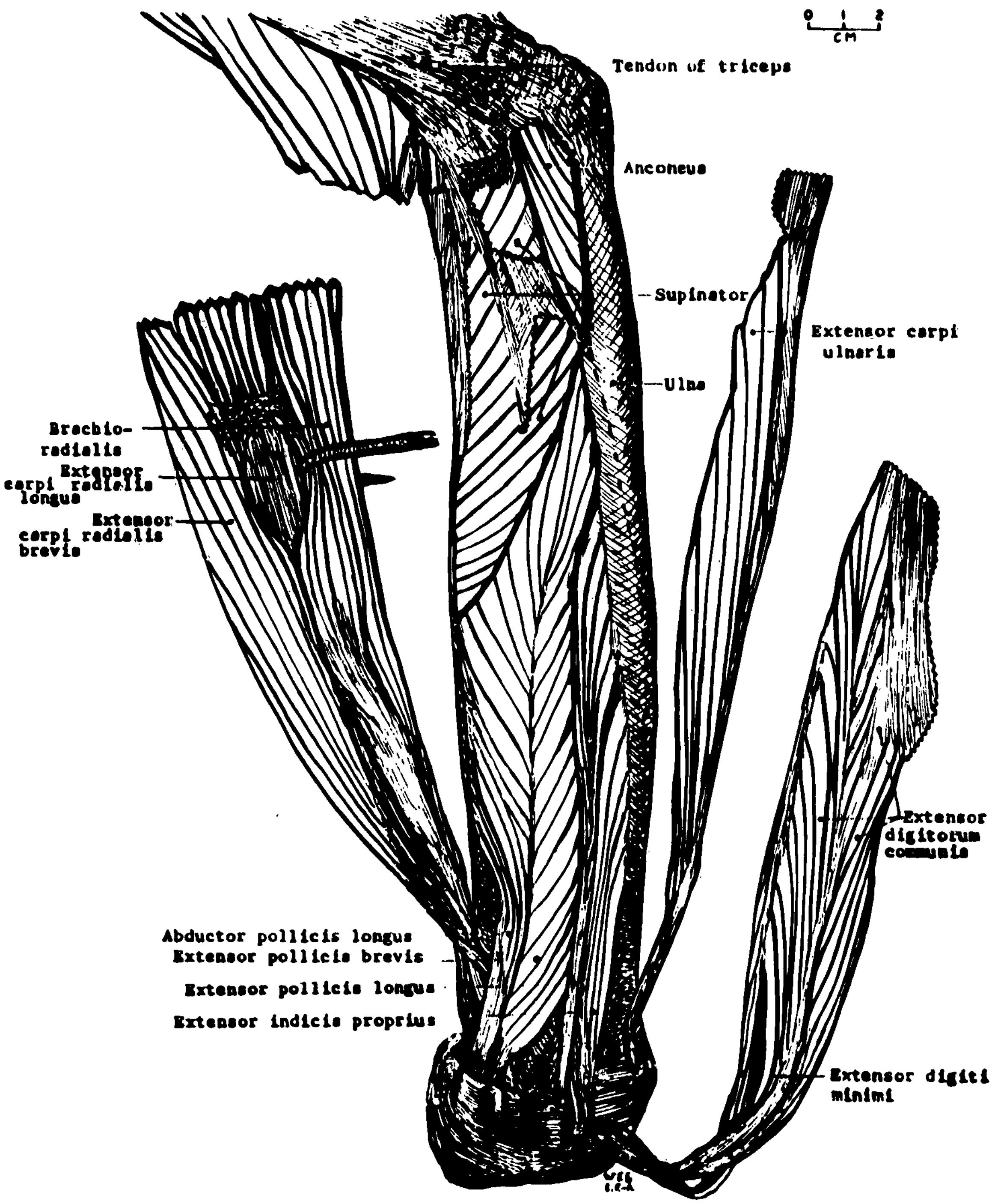

Figure 15

Posterior View of Antebrachium with Brachioradialis, Extensors Carpi Radialis Longus and Brevis, Extensor Digitorum Communis, Extensor Digiti Minimi, and Extensor Carpi Ulnaris Displaced to Show Their Deep Surfaces and Underlying Structures

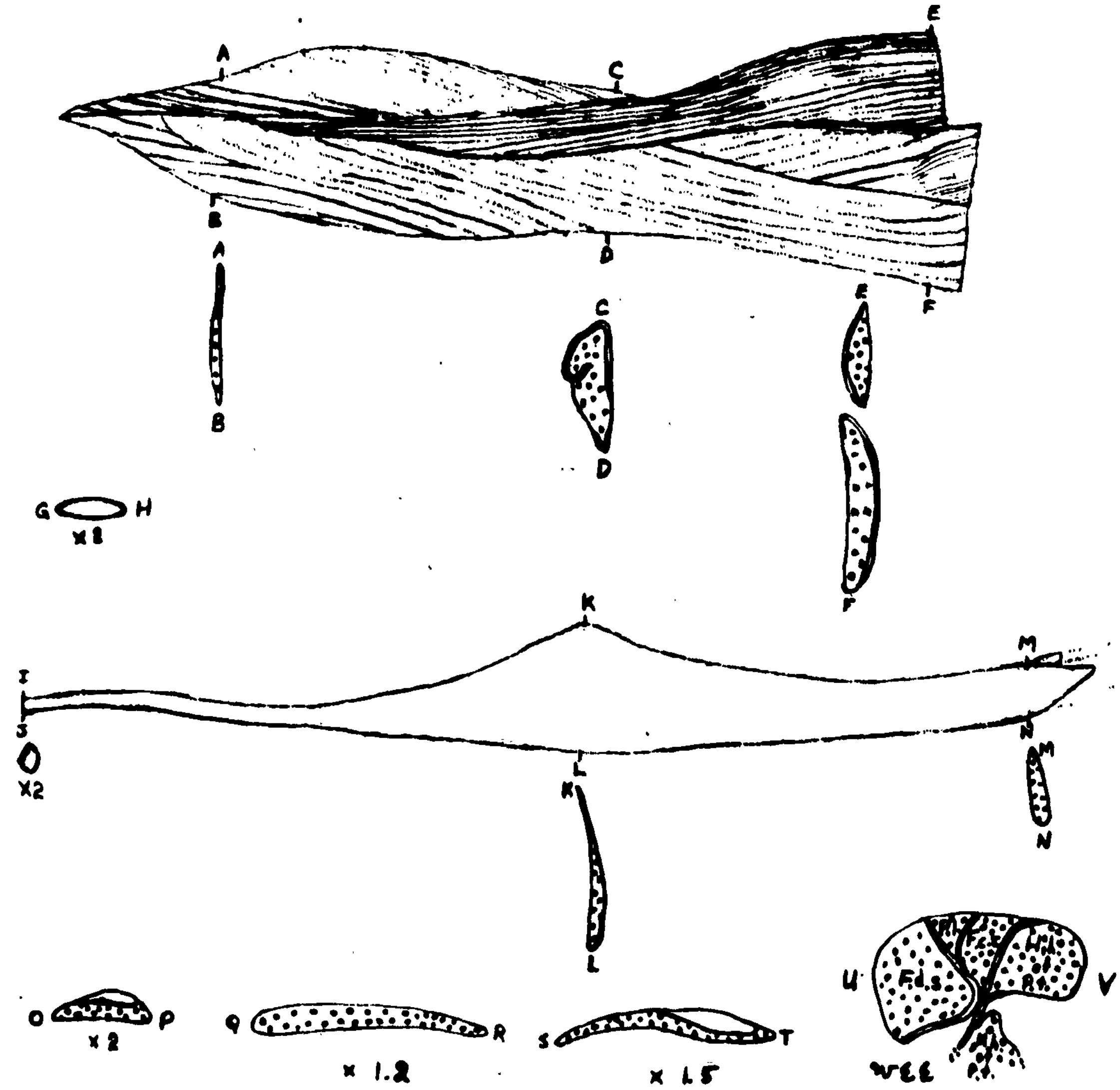

Figure 16

Cross-Sections of Superficial Flexors

Cross-sections are shown through humeral (F) and ulnar (E) heads of pronator teres (A-B, C-D, and E-F), the tendon of palmaris longus where transected distally (G-H), the ulnar head of flexor digitorum sublimis (I-J, K-L, and M-N), the deep head of flexor digitorum sublimis where transected proximally (O-P), flexor carpi ulnaris where transected proximally (Q-R) and distally (S-T), and the superficial flexors where transected near their proximal ends (U-V).

The locations of the transections are shown in the other figures where not shown here. All outlines and sections are natural size except U-V and where otherwise indicated. In both outlines proximal is to the right. All sections are shown as viewed from distal to proximal except A-B, C-D, and E-F. All sections have been drawn quite precisely except U-V, which was roughly sketched.

Stippled zones of sections represent fleshy portions; unfilled zones represent tendon.

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1 ORIGINATING ACTIVITY (Corporate author) William E. Edwards	2a REPORT SECURITY CLASSIFICATION Unclassified
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3 REPORT TITLE STUDY OF MONKEY, APE, AND HUMAN MORPHOLOGY AND PHYSIOLOGY RELATING TO STRENGTH AND ENDURANCE - PHASE V: THE MUSCULOSKELETAL ANATOMY OF THE ANTEBRACHIUM OF AN ADULT FEMALE CHIMPANZEE

4 DESCRIPTIVE NOTES (Type of report and inclusive dates)
Final 1961-1963

5 AUTHOR(S) (Last name, first name, initial)
Edwards William E.

6 REPORT DATE	7a TOTAL NO OF PAGES	7b NO OF REFS
April 1965	40	23

8a CONTRACT OR GRANT NO. AF 29(600)-3466	9a ORIGINATOR'S REPORT NUMBER(S) ARL-TR-65-4
b PROJECT NO 6892	
c Task No. 689201	9b OTHER REPORT NO(S) (Any other numbers that may be assigned this report)
d	

10 AVAILABILITY/LIMITATION NOTICES

11 SUPPLEMENTARY NOTES	12 SPONSORING MILITARY ACTIVITY 6571st Aeromedical Research Laboratory Holloman AFB, New Mexico

13 ABSTRACT

The left antebrachial musculature of a young-adult female chimpanzee is described and illustrated with the accuracy of detail plus clarity made possible by the photo-etching process. Other data are depicted graphically by section drawings. Comparisons with data from the literature on other chimpanzees, apes, humans, and non-hominoid primates are also provided, with emphasis on quantitative aspects.

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